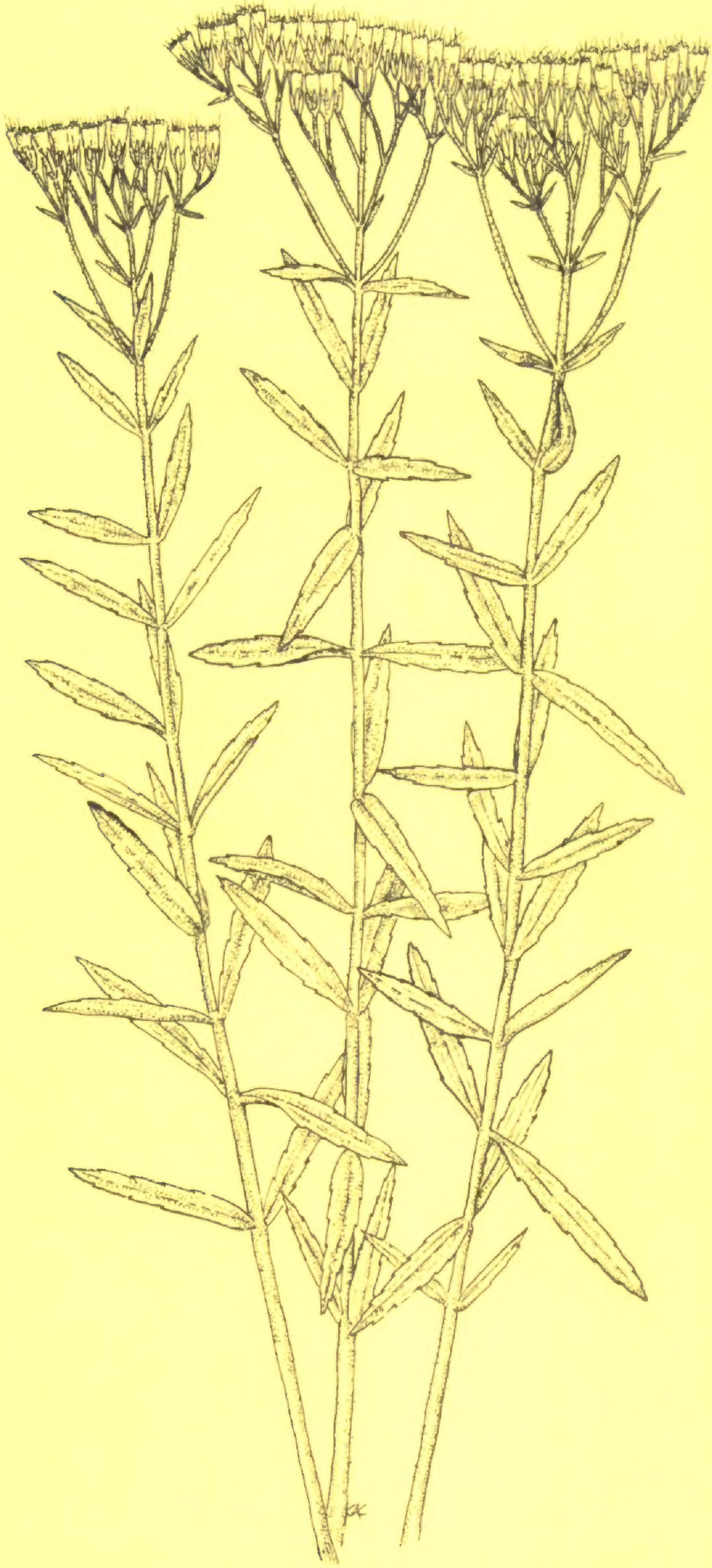
Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB



Vol. 90 January 1988 No. 861

The New England Botanical Club, Inc.

22 Divinity Avenue, Cambridge, Massachusetts 02138

RHODORA

NORTON H. NICKERSON, Editor-in-Chief

Associate Editors

DAVID S. BARRINGTON
A. LINN BOGLE
DAVID E. BOUFFORD
WILLIAM D. COUNTRYMAN
GARRETT E. CROW
RICHARD A. FRALICK
GERALD J. GASTONY
C. BARRE HELLQUIST
MICHAEL W. LEFOR
ROBERT T. WILCE

ISSN 0035-4902

RHODORA.—Published four times a year, in January, April, July, and October by the New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138. Second Class postage paid at Boston, MA. A journal of botany devoted primarily to the flora of North America. Price $25.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to 22 Divinity Avenue, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related areas, and articles concerned with systematic botany and cytotaxonomy in their broader implications will be considered. Brevity is urged; please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Fifty reprints of each article are supplied free of charge. Authors may arrange with Lexington Press for additional copies. RHODORA assesses page charges.

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

POSTMASTER: Send address changes to RHODORA, 22 Divinity Avenue, Cambridge, MA 02138.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS 02173

Cover Illustration

Eupatorium leucolepis var. *novaeangliae* is an endemic New England taxon restricted to upper margins of sandy-peaty coastal plain ponds. Currently vouchered from 7 ponds in MA and 5 in RI (several historical stations are extirpated), New England Boneset is a candidate for federal listing. The nominate variety occurs from Long Island in NY (very rare) and southern NJ to FL and LA.

Original artwork by Caren Caljouw

Rhodora

(ISSN 0035-4902)

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 90 January 1988 No. 861

REGROWTH OF A DECIMATED POPULATION OF *PANAX QUINQUEFOLIUM* IN A MISSOURI CLIMAX FOREST

WALTER H. LEWIS

ABSTRACT

A population of *Panax quinquefolium* was decimated by ginseng diggers in 1979, although most components of the climax forest community remained unaltered. After five years, 79% of the population size had been restored of which 25% were flowering plants; from these, 47 fruits matured. By 1985, 39% of the population consisted of flowering plants. The most logical assumption is that a majority of the new population originated from an *in situ* seed bank holding sufficient viable seeds to re-establish a large portion of the population until plants of the "new population" had become reproductive. Seeds of this herbaceous perennial apparently remained dormant and viable in the soil for at least five years, thus providing an adaptive mechanism for population restoration following major disruption and perhaps also adverse seasonal environmental conditions.

Key Words: *Panax quinquefolium,* American ginseng, seed bank, population restoration, Missouri

INTRODUCTION

In 1978 a population of *Panax quinquefolium* L. (American ginseng) was marked for study in an oak-hickory community of the Ozark Plateau, southwestern Missouri (ca. 60 m^2 area in Magnolia Hollow, Taney Co., *Lewis 9098* MO). The species is a long-lived herbaceous perennial, a geophyte, found infrequently in the shaded understory of this climax deciduous forest, appearing after the leaf canopy has partially or fully developed, and flowering and fruiting during the summer months. Asexual reproduction due to rhizome/root fragmentation is very rare and unknown in most populations.

Fruits rarely form before a plant is three years old and often plants are much older before fruiting (Lewis and Zenger, 1982). The fruit is typically a two-seeded (pyrenes) drupe that is globose, about 1 cm in diameter; it develops a bright red exocarp and a stony endocarp at maturity. The seed is about 3 mm long, subglobose, and requires an after-ripening that averages 20 months (Lewis and Zenger, 1982).

The original population consisted of 98 plants of which 66% had inflorescences with 2 to 4 prongs or whorls of leaflets (9–20 leaflets), and the remainder were juveniles having 1 or 2 prongs (3–9 leaflets). There were four prong classes: 1-pronged juveniles made up 26% of the population, 3-pronged flowering plants were in the majority (50%), and 2- and 4-pronged plants were less frequent (12% and 13%, respectively). Even though plants were not individually aged, a long-time resident of the area had observed the undisturbed population for 18 years. As age of plants (determined by counts of annual bud scars) is significantly correlated with prong class elsewhere in Missouri (Lewis and Zenger, 1982) and in New York (Lewis, 1984), the majority of 1-pronged plants were probably 1 to 3 years old, 2-pronged plants were 2 to 10 years old, 3-pronged plants were 3 to at least 20 years old, and 4-pronged plants were 13 years of age and undoubtedly much older. The morphology of the plants above ground and the informant's observations indicate a population established two decades ago, and perhaps longer, that was probably still expanding as reflected by the 26% frequency of single-pronged juveniles.

In August, 1979, the population was eradicated by diggers; only one 1-year-old plant remained, and there were no early senesced individuals present. Plants outside the study site scattered along the hollow for about 25 m were also completely removed. Apparently only American ginseng was dug, for other perennials that covered much of the area, such as *Asarum canadense* L., *Arisaema atrorubens* (Ait.) Blume, and *Hepatica nobilis* Schreb., along with weedy *Parthenocissus quinquefolia* (L.) Planch. and *Toxicodendron radicans* (L.) Kuntze, showed limited disturbance, and the densely shaded habitat as a whole remained intact. Nevertheless, the soil was completely disrupted where the usually deep and branched ginseng roots had been removed. The site was re-examined in July, 1984, and June, 1985.

It must be emphasized that other populations of *Panax quinquefolium* did not occur in the vicinity of this hollow nor for distances of at least three miles in all directions. Indeed, the species is now extremely rare in the whole region.

RESULTS AND DISCUSSION

After five years, 77 plants or 79% of the original population size had been re-established. The one juvenile remaining in 1979 was located along with 76 additional plants, the latter ranging in age from 1 to 5 years based on counting annual rhizomatous bud scars (Table 1). Surviving plants in 1984 included 2 plants from 1980, one year after the decimation, 11 and 9 from 1981 and 1982, respectively, and 27 plants from both 1983 and 1984. About one-quarter were flowering and these produced 47 fruits, illustrating a modest reproductive capacity after 5 years.

What was the origin of the propagules that gave rise to the "new population"? As the few scattered plants elsewhere in the hollow were also eradicated, they could not have been the source. No *Panax quinquefolium* was observed for miles in the vicintiy of the hollow, so bird droppings or other animal transport were also unlikely sources of so many propagules. As rhizome/root fragmentation is extremely rare in the species, regeneration of this population by asexual means would have been impossible. The single 1979 survivor could have produced fruits in 1981 with seeds germinating by 1983, and again in 1982 with germination in 1984, but extrapolating from this plant's 1984 fruit production, I estimate that only a

Table 1. Population structure in 1984 of 77 plants* of *Panax quinquefolium* re-established in Taney Co., MO, after almost complete eradication during August 1979.

Age	Yr. cohort established	No. of plants established by year	Prongs per plant (average)	Leaflets per plant (average)	Flowering plants (%)	No. of Fruits
1	1984	27	1.0	3.0	0	0
2	1983	27	1.3	5.4	4	1
3	1982	9	2.3	10.3	67	9
4	1981	11	2.9	14.3	100	29
5	1980	2	2.5**	10.5**	50**	2
6***	1979	1***	3.0	15.0	100	6

*In 1985 there were 74 plants; since 10 were new seedlings, only 64 remained from the 1984 total of 77; therefore, 13 had died between July 1984 and June 1985 (69% were 1-yr. old seedlings).
**One of two extant plants was only 2-pronged, with 6 leaflets and no flowers.
***The only plant known to have survived the population destruction of 1979; it was then 1 year old.

maximum of 10 seeds could have been produced during these years. The chances that all survived and germinated is very slight because of high seed vulnerability in the life cycle (Lewis and Zenger, 1982), but a few may have done so. Based on numbers of seedlings formed annually, however, it is assumed that the great majority of plants developed from a pre-eradication seed bank at the site, and it certainly was the source of almost all seeds that germinated between 1980 and 1983. By 1984, seedlings could have formed from the seed bank as well as from the single survivor and even re-established plants of which a very few were probably reproductive in 1982.

In June, 1985, before fruit maturation (and the only time I could visit the population in that year), 74 plants were found at the site, including 10 new seedlings (14%). Of the 13 plants that had died, nine were one-year-old seedlings (Table 1), a particularly vulnerable age during the unusually dry late summer and early fall months of 1984. However, the marked reduction of new plants compared to 1983 and 1984 suggests that limited numbers of viable seeds remained in the seed bank by 1985, although some other factors, such as changed environmental conditions for seed germination, could have been involved in seedling reduction. In fact, the reduced frequency of seedlings in 1985 is all the more dramatic since some propagules from the re-established population would have been expected by then. Indeed, the maturation of the new population is well illustrated by the increased number of flowering plants from 19 (25%) in 1984 to 29 (39%) in 1985.

In 1984 and 1985, a few scattered plants were observed elsewhere in the hollow, all in close proximity to sites where plants existed prior to August, 1979. These observations support evidence from the primary site that most seeds entered the soil very near the parent plants. No new plants were found in areas not previously populated by ginseng, further suggesting limited dispersibility of seeds in this forest community.

Large numbers of seeds lie dormant in most soils; in particular, seeds of many early successional herbs accumulate in great numbers, have the capacity for longevity, and often germinate following major or local disturbances (Cook, 1980; Cook and Lyons, 1983). In mature forests, according to Cook (1980), seeds of climax species may exist in small proportions or be lacking altogether. Even though seeds of late successional *Panax quinquefolium* apparently accumulate in the forest seed bank, their numbers are probably not large not do they remain viable for prolonged periods, or both, for after five years new seedlings generated from this source were greatly reduced. Nevertheless, during this time nearly 80% of

the original population size had been restored, and by the sixth year almost 40% of the plants were flowering, with potential capability of sustaining the population by seeds for an extended period.

The most logical assumption is that *Panax quinquefolium* was restored where decimated because viable propagules in sufficient numbers had accumulated in a seed bank, and probably also because the essential components of the habitat remained. The capacity of seeds to stay dormant and viable in the soil is an important feature of species, a property believed by Cook (1980) to be a product of natural selection and therefore adaptive. Such a contention is supported by this study, for not only did the seed bank lead to restoration of the population, but these seed reserves may be relevant during adverse environmental conditions, such as summer drought when fruit production is markedly reduced (Lewis and Zenger, 1982). Thus annual recruitment need not vary significantly in an otherwise stable, long-lived population.

ACKNOWLEDGMENTS

This research was supported by a grant from the Missouri Department of Conservation; to Mr. John E. Wiley and Dr. James H. Wilson of that Department I am grateful for their continued assistance. Special thanks go to Ralph W. Lucas of Branson, Missouri, who accompanied me in the field and who, with his wife, Virginia G. Lucas, deeded the property containing the study population to the School of the Ozarks for long-range education and conservation purposes. I thank Doctors Robert Cook and Barbara Schaal for their comments on the manuscript.

LITERATURE CITED

Cook, R. 1980. The biology of seeds in the soil, pp. 107–129. *In:* O. T. Solbrig, Ed., Demography and Evolution in Plant Populations. University of California Press, Berkeley.

——— and E. E. Lyons. 1983. The biology of *Viola fimbriatula* in a natural disturbance. Ecology 64: 654–660.

Lewis, W. H. 1984. Population structure and environmental corollaries of *Panax quinquefolium* (Araliaceae) in Delaware County, New York. Rhodora 86: 431–437.

——— and V. E. Zenger. 1982. Population dynamics of the American ginseng *Panax quinquefolium* (Araliaceae). Amer. J. Bot. 69: 1483–1490.

DEPARTMENT OF BIOLOGY
WASHINGTON UNIVERSITY
ST. LOUIS, MISSOURI 63130

RHODORA, Vol. 90, No. 861, 1988

PAPAVER L. SECT. *CALIFORNICUM* KADEREIT, A NEW SECTION OF THE GENUS

JOACHIM W. KADEREIT

ABSTRACT

Papaver californicum, the only annual species of the genus *Papaver* native to North America is described and mapped. Because of the annual habit, color of filaments and valvate capsules it is placed in a section of its own, sect. *Californicum* Kadereit, which is described here. The species is suggested to have differentiated from the same stock as the perennial arctic-alpine sect. *Meconella*.

Key Words: Papaveraceae, *Papaver*, *Papaver* sect. *Californicum*, *Papaver californicum*, *Papaver* sect. *Meconella*, California

INTRODUCTION

Among the annual species of the genus *Papaver* L., *P. californicum* A. Gray is the only one native to North America. Other annuals found in America, but clearly of introduced status, are *P. rhoeas* L. and *P. dubium* L. of sect. *Rhoeadium* Spach, *P. hybridum* L. of sect. *Argemonidium* Spach and *P. somniferum* L. subsp. *somniferum* of sect. *Papaver* (Kiger, 1975). Fedde (1909), in his revision of the Papaveraceae, included *P. californicum* in sect. *Rhoeadium* alongside Old World annuals with glabrous capsules and sessile though not amplexicaulous upper stem leaves.

In the present account, besides presenting a description of *Papaver californicum* and its distribution, basic differences are pointed out between this species and the Old World annuals which justify the accommodation of *P. californicum* in a section of its own. The isolated geographical position of *P. californicum* is also discussed. Altogether, 48 herbarium specimens of *Papaver californicum* from B, BM, CAS, DS, G, GH, M and NDG were examined.

Papaver californicum A. Gray, Proc. Amer. Acad. Arts 22: 313 (1887) TYPE: U.S.A. California, Santa Inez Mountains. *J. Spence s.n.* (GH!)

SYN.: *Papaver lemmonii* Greene, Pittonia 1: 168 (1888) TYPE: U.S.A. California. S. Luis Obispo Co., *Lemmon s.n.* (NDG!)

Erect annual herbs, 12.0–65.0 cm high, unbranched below to branched from the base. All green parts with mostly sparse indumentum of patent setae. Leaves 0.9 × 0.5–15.0 × 4.5 cm; lower leaves petiolate, petiole up to 7.0 cm long; leaves increasingly sessile and decreasing in size towards the apex; leaves narrowly obovate to broadly ovate in outline, 1- 2-pinnatipartite; segments obovate to oblong, ovate or triangular in outline, antrorse, pinnatipartite to incised to entire; ultimate segments mostly obtuse; indumentum mostly stronger on lower surface.

Flowers in mostly many-flowered racemose inflorescenses; flower buds 0.6 × 0.4–1.0 × 0.7 cm shortly before anthesis, ovoid, ellipsoid, obovoid or almost globose, obtuse. Petals broadly to narrowly obovate, 0.6 × 0.3–2.1 × 2.0 cm, outer pair mostly broader than inner; petals light orange with greenish or yellowish base. Stamens many, 6.5–11.0 mm long; filaments filiform, yellow, transparent; anthers 0.5–1.5 mm long, oblong, yellow; stamens as long as to shorter than ovary; ovary almost globose; stigmatic disc with 4–8 stigmatic rays, distinctly narrower than ovary, conical to umbonate; free lobes of stigmatic disc scarious, overlapping. Capsule (Figure 1) 9.0 × 5.0–18.0 × 8.0 mm, ellipsoid to obovoid, valvate, dehiscing along placentae from below stigmatic disc to up to 1/4 of total length; valves slightly recurved; stigmatic disc umbonate in fruit, margin of disc often bent upwards and often as high as umbo; ovary and capsule frequently with 2 stigmatic discs. Seeds 0.5 – 0.7 mm long, reniform, black, matt.

Flowering March to May. Mostly found in burns, less often in disturbed ground. The geographical distribution of *Papaver californicum* is shown in Figure 2. Ernst (1958) reported its chromosome number as $2n = 28$.

Papaver sect. *Californicum* Kadereit

Among the annual species of *Papaver, P. californicum* is one of two species with yellow instead of black filaments. The other species showing this character is *P. aculeatum* Thunb. which, by its occurrence in South Africa and Australia (probably as an introduction in the latter continent) is just as aberrant geographically as is *P. californicum*. *Papaver californicum* differs from *P. aculeatum*, the only representative of sect. *Horrida* Elkan, in its distinctly valvate capsule dehiscense. Here, triangular valves are formed at capsule maturity through basipetal dehiscense along the placentae, while in *P. aculeatum* (and all other species with poricidal capsules) the regular basipetal retraction of the carpel backs leads to rectangular or square pores without distinct valves. *Papaver aculeatum* also has

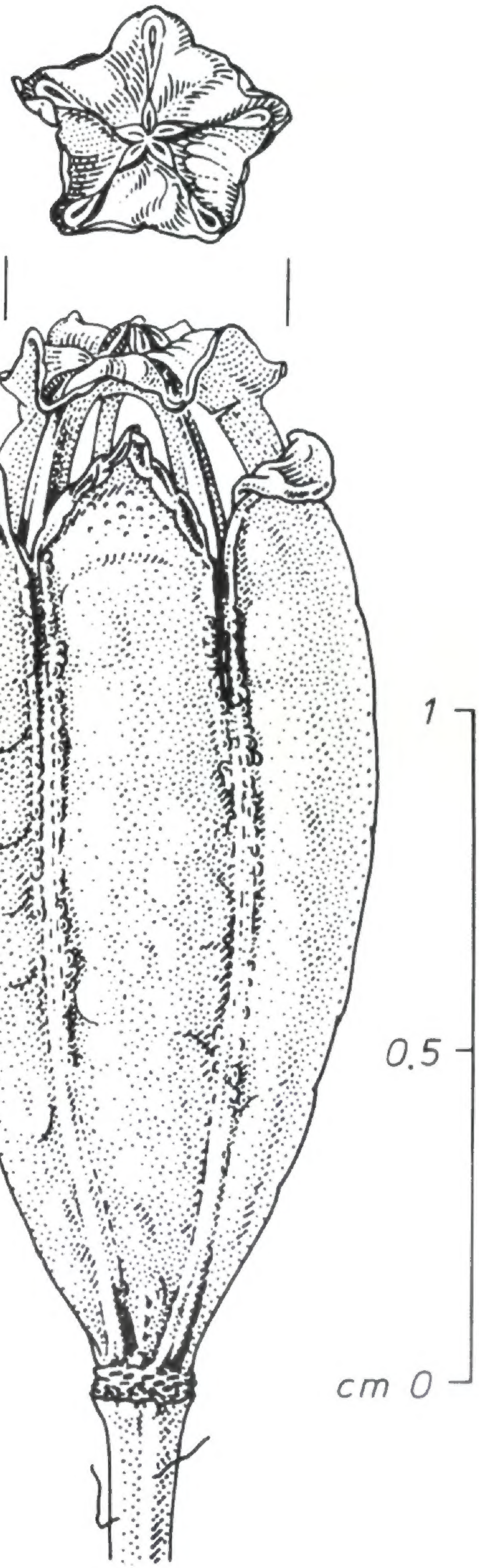


Figure 1. Mature capsule of *Papaver californicum*.

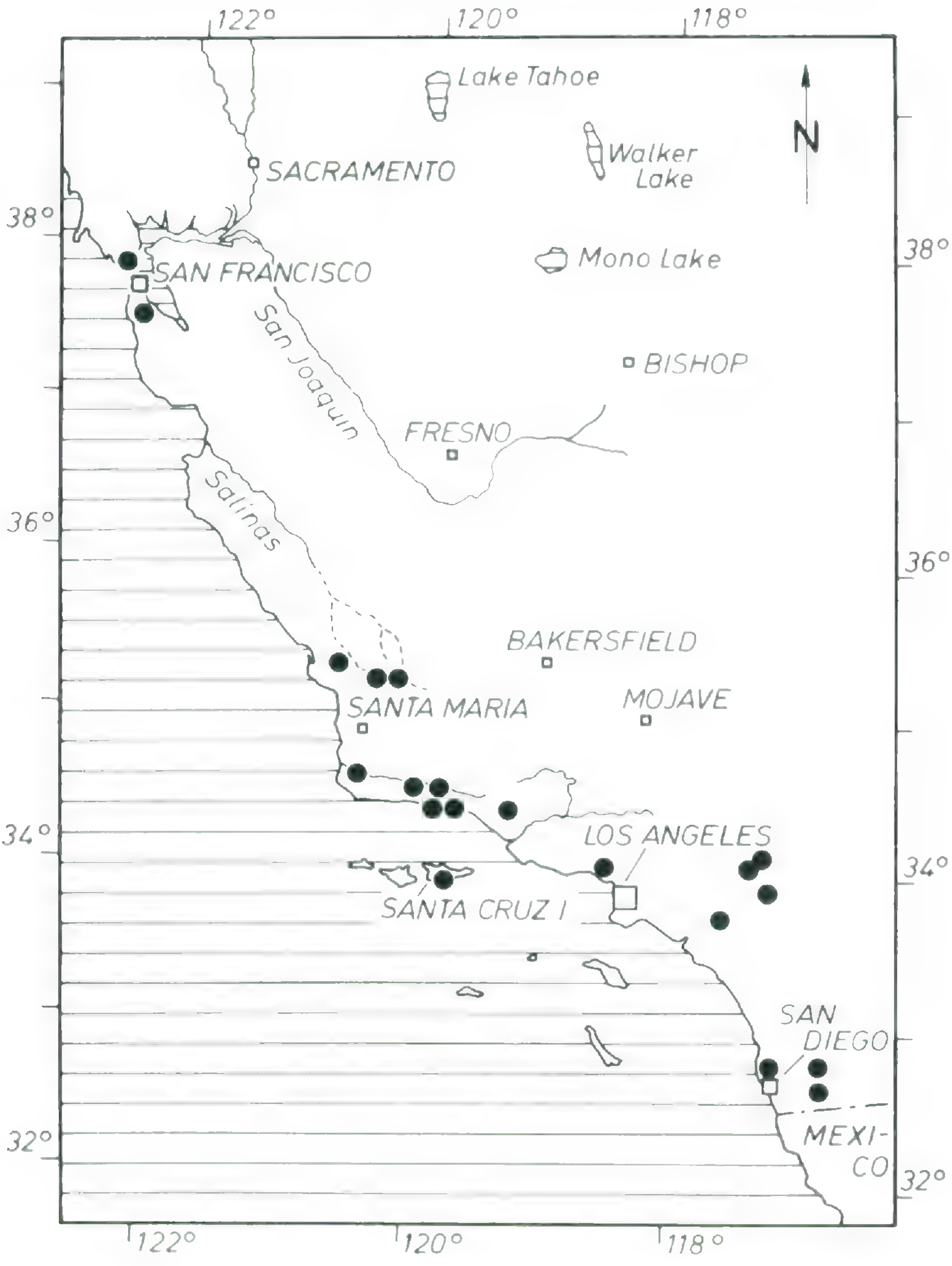


Figure 2. Geographical distribution of *Papaver californicum*.

a flat stigmatic disc, which is conical to umbonate in *P. californicum*. *Papaver californicum* differs from sect. *Rhoeadium*, in which it was included by Fedde (1909), in its valvate capsules and the color of its filaments. The capsules of sect. *Rhoeadium* are poricidal and the filaments are black. The same differences can be observed in comparison with sect. *Papaver*, which differs from sect. *Rhoeadium* only in its amplexicaulous upper cauline leaves. Section *Carinatae*

Fedde has black filaments and capsules with a deciduous stigmatic disc, and sect. *Argemonidium,* the last of the annual sections of the genus, has bristly capsules and again black filaments. On account of the annual habit, the inclusion of *P. californicum* within any of the biennial or perennial sections of the genus need not be considered, although as will be discussed below, the relation of *P. californicum* to some of these certainly is closer than to any of the annual sections.

In view of the above combination of characters, i.e. yellow filaments, valvate capsules and annual habit, *Papaver californicum* clearly deserves to be placed in a separate section, in accordance with the existing sectional concepts in the genus.

With regard to valvate capsule dehiscense, this character was already noticed by Gray (1887), who also described that the valves eventually break off at maturity. The material seen by the author does not confirm this observation. Capsules from a separate envelope on the type specimen, however, show this phenomenon, possibly due to mechanical damage.

Papaver sect. **Californicum** Kadereit, *sect. nov.*

Herbae annuae erectae, sparsim patenter setosae in partibus viridibus; folia 1- 2-pinnatipartita; petala aurantiaca, basi viridula vel flavida; stamina numerosa, filamentis filiformibus, luteis, translucidis, antheris oblongis, luteis; capsulae glabrae, ellipsoideae vel obovoideae, 4–8-valvis dehiscentes, valvis se extendentibus usque ad quartam superiorem longitudinis totae; disci stigmatis fructu umbonati.

Type: *Papaver californicum* A. Gray

Geographical considerations

Although *Papaver californicum* is the only annual poppy in North America, it is not the only representative of the genus on that continent. There also exist a number of perennial species of sect. *Meconella* Spach (=*Lasiotrachyphylla* Bernh., sect. *Scapiflora* Elkan) mainly in arctic latitudes, but including *P. pygmaeum* Rydb. and *P. kluanense* D. Löve from the Rocky Mountains (Rändel, 1975) as the southernmost representatives. *Papaver californicum* is similar to this group in color of filaments and anthers, which are either yellow or white in sect. *Meconella.* Also, the capsules are valvate in this group, though not as distinctly as in *P. californicum.* Both these characters, however, must be regarded as primitive for the genus and accordingly may not testify to the close affinity

between the two groups. Thus, except in the genus *Roemeria* Medic. and in sections *Papaver, Rhoeadium, Carinatae, Argemonidium* and *Macrantha* Elkan (=*Oxytona* Bernh.), the filaments are almost always white or yellow in the Papaveraceae, and valvate capsule dehiscense is characteristic for most genera. The similarity of *P. californicum* is stronger to sect. *Meconidium* Spach (=*Milthanta* Bernh., sect. *Pyramistigmata* Elkan), a group of biennials centered in the Caucasus. In addition to the coloration of the stamens and the valvate capsules, these latter two groups also share the umbonate to strongly conical stigmatic disc.

From the work of Rändel (1974) it is possible to develop a detailed hypothesis on the geographical history of sect. *Meconella.* Because diploid taxa of this group occur in inner Asia, at high altitudes in Europe (*Papaver alpinum* L. s.l.) and in the Rocky Mountains (*P. pygmaeus*), it seems likely that sect. *Meconella* attained its wide geographical distribution at the diploid level, i.e., as a genomically uniform group. Accordingly, genomic differentiation (up to 12x taxa are known in this group) may have taken place only after, and not during the process of geographical expansion.

It seems possible that *Papaver californicum* and the Caucasian sect. *Meconidium* have differentiated from the same stock as sect. *Meconella.* From the existence of species of the latter group in arid habitats in inner Asia (e.g. *P. croceum* Ledeb.), which are regarded as being primitive (Tolmacev, 1960 in Rändel, 1974), it may be concluded that this widespread stock existed under more arid conditions than at present, conditions closer to those in which *P. californicum* and sect. *Meconidium* are found than to those of the mainly arctic-alpine species of sect. *Meconella.* Accordingly, since *P. californicum* is a tetraploid (Ernst, 1958) and sect. *Meconidium* seems to consist mainly of diploids (Federov, 1969; Caine, 1977, Ph.D. thesis, Univ. of Liverpool), these two groups seem to have undergone less genomic change than the taxa of sect. *Meconella.* The affinity of *P. californicum* to sects. *Meconella* and *Meconidium* has also been suggested by Markgraf (1958).

Finally, it may be of interest from a phytogeographical point of view to note that *Stylomecon heterophylla* (Benth.) G. Taylor, originally described as a member of the mainly Himalayan genus *Meconopsis* Vig. and with obvious affinities to it, is the only representative of this group in North America and has a distributional range very similar to that of *P. californicum.* Thus in both cases mainly asiatic groups contain a taxonomically somewhat isolated representative in western North America. While in *Papaver* sect.

Meconella constitutes a geographical link, no such link exists between *Stylomecon* G. Taylor and *Meconopsis* (a genus closely related to *Papaver*).

ACKNOWLEDGMENTS

I express my thanks to the directors of B, BM, CAS, DS, G, GH, M and NDG for the loan of herbarium material, to Mr. F. Rückert for the preparation of the figures, and to Prof. P. Leins for critically reading the manuscript.

LITERATURE CITED

ERNST, W. R. 1958. Chromosome numbers of some western Papaveraceae. Contr. Dudley Herb. 5: 109–115.

FEDDE, F. 1909. Papaveraceae-Hypecoideae et Papaveraceae-Papaveroideae. *In:* Engler, A., Ed., Das Pflanzenreich 40(4, 104): 1–430. Leipzig.

FEDEROV, A. 1969. Chromosome numbers of flowering plants. Leningrad.

GRAY, A. 1887. XV. Contributions to American Botany. Proc. Amer. Acad. Arts 22: 270–314.

KIGER, R. W. 1975. Papaver in North America north of Mexico. Rhodora 77: 410–422.

MARKGRAF, F. 1958. Papaveraceae. *In:* Hegi, G., Ed., Illustrierte Flora von Mitteleuropa ed. 2, IV 1/2: 15–49.

RÄNDEL, U. 1974. Beiträge zur Kenntnis der Sippenstruktur der Gattung Papaver L. sectio Scapiflora Reichenb. (Papaveraceae). Feddes Repert. 84: 655–732.

———. 1975. Die Beziehungen von Papaver pygmaeum Rydb. aus den Rocky Mountains zum nordamerikanischen P. kluanense D. Löve sowie zu einigen nordost-asiatischen Vertretern der Sektion Scapiflorae Reichenb. im Vergleich mit P. alpinum L. (Papaveraceae). Feddes Repert. 86: 19–37.

TOLMACEV, A. I. 1960. Der authochthone Grundstock der arktischen Flora und ihre Beziehungen zu den Hochgebirgsfloren Nord- und Zentralasiens. Bot. T. 55: 269–276.

INSTITUT F. SYSTEMATISCHE BOTANIK U.
PFLANZENGEOGRAPHIE
IM NEUENHEIMER FELD 328
6900 HEIDELBERG
FRG

RHODORA, Vol. 90, No. 861, 1988

THE TAXONOMIC STATUS OF *POTAMOGETON LATERALIS* MORONG (POTAMOGETONACEAE)

C. Barre Hellquist, C. Thomas Philbrick,
and Robert L. Hilton

ABSTRACT

Potamogeton lateralis is believed to be one of the rarer pondweeds of North America. Evidence is provided indicating that *P. lateralis* is in fact described from two disparate elements, *P. vaseyi* and *P. pusillus*. The morphological characters of *P. lateralis* fit well within the range of these two species.

Key Words: *Potamogeton lateralis, P. vaseyi, P. pusillus*, synonym, lectotype

Since first being described by Morong (1880), *Potamogeton lateralis* Morong has been considered one of the rarest North American pondweeds. Ogden (1974) raised some question concerning the validity of the taxon when he stated that "*P. lateralis* was apparently closely related to *P. vaseyi* and may merely be a variant of that species." This issue has not been pursued subsequently in the literature. Concern regarding the rarity of *P. lateralis* persists, as exemplified by the inclusion of this taxon on various regional rare and endangered species lists such as Crow et al., 1981. The purpose of this paper is to present evidence that the rarity of *P. lateralis* is actually synonymous in part with *P. pusillus* L. and *P. vaseyi* Robbins.

A paucity of information in Morong's protolog (Morong, 1880) for *Potamogeton lateralis* makes taxonomic investigation difficult. When Morong described *P. lateralis* he failed to designate a holotype. The type concept was not formalized at that time; therefore, it is unclear what specimen(s) he used to describe the taxon. Furthermore, Morong made no reference to the specific locality from which the specimens came other than to say that *P. lateralis* was found in the Charles River, Dedham, Massachusetts. Morong did note that the plant was rare and underdeveloped specimens have been referred to *P. pusillus* L. He also added that during the previous year C. E. Faxon had collected *P. lateralis* with abundant floating leaves, leaves and fruit. Thus, we assume that Morong based his description of *P. lateralis* on Faxon's specimens that were collected in 1879 (Figure 1).

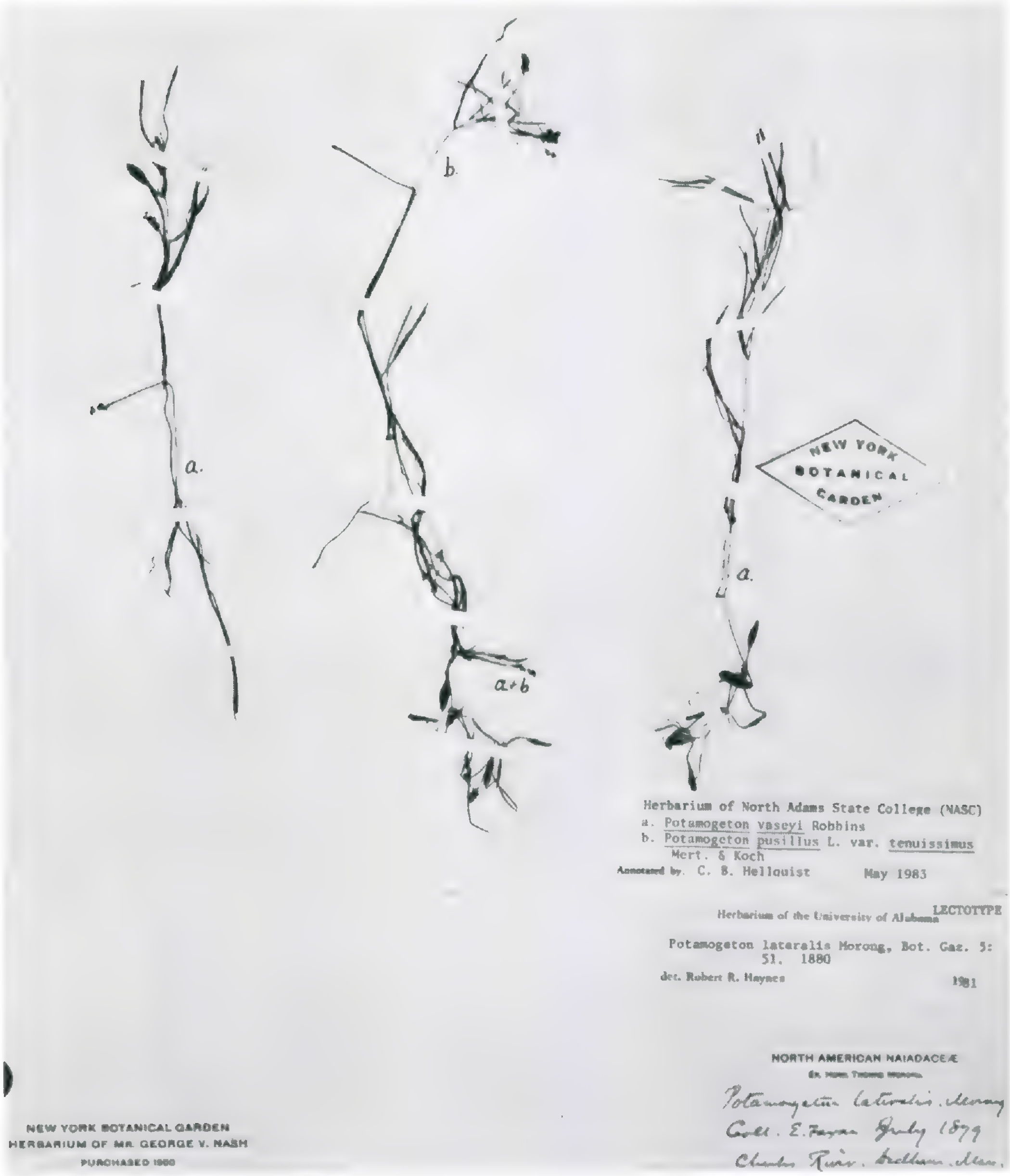

a.
b.
a+b
NEW YORK BOTANICAL GARDEN
a.
Herbarium of North Adams State College (NASC)
a. Potamogeton vaseyi Robbins
b. Potamogeton pusillus L. var. tenuissimus Mert. & Koch
Annotated by. C. B. Hellquist May 1983
Herbarium of the University of Alabama
LECTOTYPE
Potamogeton lateralis Morong, Bot. Gaz. 5: 51. 1880
det. Robert R. Haynes 1981
NEW YORK BOTANICAL GARDEN
HERBARIUM OF MR. GEORGE V. NASH
PURCHASED 1950
NORTH AMERICAN NAIADACEÆ
Potamogeton lateralis. Morong
Coll. E. Faxon July 1879

Figure 1. A representative sheet of the Faxon collections from which Morong described *Potamogeton lateralis*. The sheet is made up disparate elements of *P. pusillus* and *P. vaseyi*, as denoted by the annotation label of Hellquist (May, 1983). It is also evident that Haynes annotated this sheet as the lectotype of *P. lateralis*.

Added confusion arises from the presence of two sets of specimens that were collected by Faxon in 1879: 13 July 1879, Dedham, MA, E. Faxon & C. E. Faxon, *s.n.*, and July, 1879, Dedham, MA, E. Faxon *s.n.* It is unclear whether these represent the same or different collections. Because both sets of sheets are virtually identical in the form of the specimens, we treat them as a single collection. (From here onward we will refer to both sets collectively as the "Faxon specimens.")

MATERIALS AND METHODS

Faxon's collections of *Potamogeton lateralis* from Dedham, MA were examined. Collections designated as *P. lateralis* and those of *P. vaseyi* and *P. pusillus* were also examined from CAN, CM, GH, MO, MSC, NASC, NEBC, NY, PH, VT, WIS, and from the personal collection of W. D. Countryman. Characters measured were those mentioned by Morong (1880) as well as those that might help clarify distinctions between *P. lateralis, P. pusillus,* and *P. vaseyi.* These latter characters were used by Fernald (1932) in his monograph of the *Potamogeton* section *Axillaries,* which includes *P. lateralis.* For field studies, six populations of *P. lateralis* and *P. vaseyi* were observed over the past 13 years: Lake Elmore, VT (1978, 1980, 1981, 1984); Lake Fairlee, VT (1972, 1981); Bellow Falls, VT (1981, 1984); Lancaster, NH (1972, 1973, 1974, 1978; Ossipee Lake, NH (1984); and Sugar Island, MI (1985). Voucher specimens from each population are deposited at NASC.

RESULTS AND DISCUSSION

Morong's (1880) protolog for *Potamogeton lateralis* did not provide the means for distinguishing between this taxon and *P. vaseyi,* a similar species. Fernald (1932, 1950) used the following characters to distinguish the two taxa. *Potamogeton vaseyi* sets fruit only on plants that have floating leaves, whereas plants that lack floating leaves do not flower or fruit. In contrast, *P. lateralis* sets fruit only on plants that lack floating leaves. However, plants with floating leaves do flower but set no fruit (Fernald, 1932).

Leaf morphology was used by Fernald (1932) to distinguish *Potamogeton lateralis* from *P. vaseyi. Potamogeton lateralis* exhibits oblong to spathulate-obovate floating leaves and acute submersed leaves; in contrast, floating leaves of *P. vaseyi* are elliptic or narrowly obovate and the submersed leaves are bristle-tipped. Our

comparison of the Faxon specimens (*P. lateralis*) with a sample of specimens of *P. vaseyi* reveals a congruent degree of variability in leaf form in both taxa. In fact, in many cases a single specimen from either set exhibited floating leaves that fell within the range of either taxon based on Fernald's distinctions. Submersed leaves of both sets of specimens were acute-tipped in virtually all cases.

A comparison of fruit size between the Faxon specimens and *Potamogeton pusillus* reveals considerable overlap as well (Faxon specimens, 1.9–2.5 mm length × 1.4–1.6 mm width; *P. pusillus,* 2–2.5 mm length × 1.2–1.9 mm width (Fernald, 1932). Fruits from the Faxon and *P. pusillus* specimens are identical in shape.

Fernald (1932, 1950) used several additional characters that were not included in Morong's protolog for *Potamogeton lateralis* to distinguish this taxon from *P. vaseyi* and *P. pusillus*. These characters include peduncle and spike length, number of flowers per spike and lacunae number on submersed leaves. The range of variation for all of these characters exhibits significant overlap for all three taxa.

The degree of overlap that is evident in these characters on the Faxon specimens and those of *Potamogeton vaseyi* and *P. pusillus* suggests that the Faxon specimens are a mixture of the two latter taxa. Thus, if in fact Morong used the Faxon specimens on which to base his description, and all evidence indicates he did, then *P. lateralis* is based on a mixture of two previously described taxa. Therefore, *P. lateralis* is taxonomically invalid and should be rejected.

Potamogeton vaseyi and *P. pusillus* often grow together. Field studies reveal that *P. vaseyi* is a rather ephemeral, annual species that flowers, sets fruit and withers by mid-August at most localities. Furthermore, this taxon is often overlooked, or collected mixed with *P. pusillus,* until floating leaves are produced. Therefore, it is not difficult to imagine how these two taxa were included as a single, mixed collection on the Faxon specimens.

Specimens originally identified as *Potamogeton lateralis* were examined from 19 different collections while those identified as *P. vaseyi* were examined from 72 collections. A list of the above mentioned specimens may be obtained by contacting the senior author.

The lectotype designated below is the specimen designated as such by Robert R. Haynes in 1981. Because the lectotype was not published previously, we are here publishing it for formal recognition.

Potamogeton lateralis Morong

LECTOTYPE: UNITED STATES. Massachusetts. Dedham, Charles River, 13 July 1879, *E. Faxon s.n.* (NY); ISOLECTOTYPES: Dedham, Charles River, 13 July 1879 (CM, GH, HNH, NASC, NEBC, NY, PH, US, VT).

CONCLUSION

It is evident that Morong (1880) used a series of specimens that were collected by Faxon (& Faxon) from which to base his description of *Potamogeton lateralis*. Our investigations of these specimens reveal that they are in fact a mixture of *P. pusillus* and *P. vaseyi*. Therefore, *P. lateralis* is not a taxonomically valid species and should be rejected; i.e., *P. lateralis* is synonymous in part with *P. vaseyi* and in part with *P. pusillus*.

ACKNOWLEDGMENTS

We wish to thank Carroll E. Wood, Jr. and Garrett E. Crow for their help in interpreting the type specimens, Robert R. Haynes for his critical review of the manuscript, and the University of Michigan Biological Station for supporting the fieldwork during the summer of 1985.

LITERATURE CITED

CROW, G. E., W. D. COUNTRYMAN, G. L. CHURCH, L. M. EASTMAN, C. B. HELLQUIST, L. J. MEHRHOFF, AND I. M. STORKS. 1981. Rare and endangered vascular plant species in New England. Rhodora 83: 259–299.

FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton* section *Axillaries*. Mem. Amer. Acad. Arts 17: (also, Mem. Gray Herb. No. 3).

_____. 1950. Gray's Manual of Botany, 8th ed. American Book Company, New York.

MORONG, T. 1880. New species of *Potamogeton*, with notes upon some published forms. Bot. Gaz. (Crawfordsville) 5: 50–53.

OGDEN, E. C. 1974. *Potamogeton* in New York. Bull. No. 423. New York State Mus. and Sci. Ser., Albany.

C. B. H.
DEPARTMENT OF BIOLOGY
NORTH ADAMS STATE COLLEGE
NORTH ADAMS, MA 01247

C. I. P.
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY, U-43
THE UNIVERSITY OF CONNECTICUT
STORRS, CT 06268

R. L. H.
DEPARTMENT OF BIOLOGY
MASSASOIT COMMUNITY COLLEGE
BROCKTON, MA 02402

RHODORA, Vol. 90, No. 861, 1988

A FLORISTIC INVENTORY OF THE GATEWAY NATIONAL RECREATION AREA, NEW YORK - NEW JERSEY

RICHARD STALTER AND ANDREW GRELLER

ABSTRACT

Four hundred fifty specific and subspecific taxa of vascular plants are known from the Gateway National Recreation Area. These taxa are included in 80 families. The largest families are the Compositae (66 species) and Gramineae (66 species). One hundred sixty-two plants (36 percent) are exotics. Families with large numbers of exotic species are the Cruciferae (71 percent), Leguminosae (64 percent), and Caryophyllaceae (62.5 percent).

Key Words: Flora, Gateway National Recreation Area, New York - New Jersey

INTRODUCTION

The Gateway National Recreation Area, comprising slightly more than 10,788 hectares, was established by an act of Congress in October, 1972 (Figure 1); it is the largest urban park system in the United States. The present study describes the flora of three sites within the Gateway National Recreation Area: Floyd Bennett Field (FBF), New York; Fort Tilden (FT), New York; and Sandy Hook (SH), New Jersey. Floristic inventories were prepared at Sandy Hook by Chrysler (1930), McKenian (1968, Master's thesis, Newark State College, Union, New Jersey), and Stalter (1979). A report on the flora of Fort Tilden has been presented at the annual meeting of the South Carolina Academy of Science by Stalter and Lechthaler (1984), but a list of the taxa at Fort Tilden has not previously been compiled. Floristic inventories at Floyd Bennett Field have been conducted by K. Venezia, Andrew Greller, Richard Stalter and several Gateway employees.

SITE DESCRIPTIONS

Floyd Bennett Field is comprised of approximately 565 ha, and is located on the west side of Jamaica Bay on the southwest corner of Long Island. It occupies the former site of Barren Island and portions of surrounding salt marsh that were covered with urban rubble and dredge fill over a 20-year period from 1900 to 1920 (Rogers et al., 1985). Floyd Bennett Field was constructed in the 1920's. Because of limited military and civilian use since the 1930's FBF was

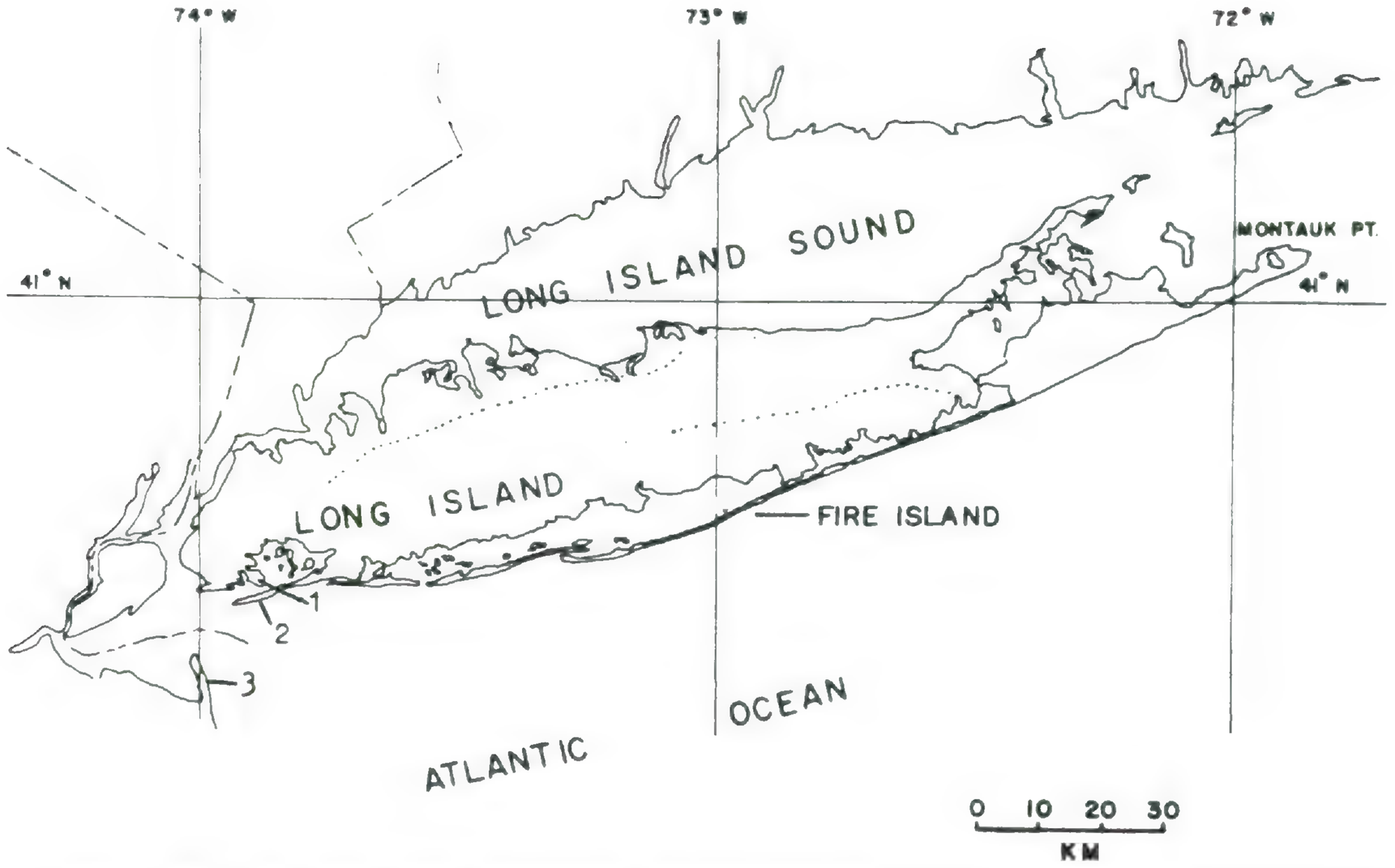


Figure 1. Map of the Gateway National Recreation Area and study sites. Site 1, Floyd Bennett Field; Site 2, Fort Tilden; Site 3, Sandy Hook (after Art, 1976).

decommissioned in 1971–72 and turned over to the National Park Service (Rogers et al., 1985). For additional historical information on FBF, see Friedberg and Partners (1980), the U.S. National Park Service (1983), and Tanacredi (1983).

Fort Tilden, encompassing 70 ha, is situated on the Rockaway Peninsula of Long Island. In 1845 the tip of Rockaway Peninsula was approximately two kilometers east of the present eastern border of Fort Tilden. From 1889 to 1985 accretion extended the Rockaway Peninsula approximately 4 kilometers west. A rock jetty was constructed to halt the western migration of the peninsula. Until Fort Tilden was constructed for military purposes, no private buildings occupied the present site of the fort. Army occupation of Fort Tilden began in 1917, when the Corps of Engineers filled marshlands behind the ocean dunes and at the east end of the reservation (Link, 1981). After the marshlands were filled, the fort was occupied by four officers and 130 enlisted men housed in hastily constructed barracks and mess halls. Plants of the area suffered further onslaught as time went on. By 1941 over 90 new barracks and supporting structures were completed. During WW II, the flora was again disturbed as 16-inch and 6-inch guns were case-mated and batteries were constructed replete with anti-anticraft guns. During the mid-1950's, Fort Tilden was used as a ground-to-air missile facility. With the advent of Intercontinental Ballistic Missiles, the facility became obsolete, and Fort Tilden was decommissioned in 1967 (Link, 1981) and the flora was left to its own devices.

Sandy Hook is a 10-kilometer-long peninsula, part of the mainland of New Jersey, 26 kilometers due south of Manhattan; it varies in width from 100 meters to 1.5 kilometers. The hook, comprised of 818 ha, is a recurved spit formed from the northerly transport of sand from eroding beaches as far south as 40 kilometers (Nordstrom et al., 1975). Since the late 1600's, the growth pattern of Sandy Hook has been well documented (Nordstrom et al., 1975). During this time period, several new hooks have been formed; older ones are now inland and newer ones are nearer the ocean. This pattern of growth is most obvious at Spermaceti and Horseshoe Coves.

METHODS

The present list of species is the result of collections and observations by numerous botanists and naturalists in each of the three areas. Stalter and his students, Debby Lechthaler, Cathy Makrinikolas and Tom Risley were responsible for collecting and identifying

the plants at Fort Tilden. Several naturalists employed by the National Park Service have collected plants at Floyd Bennett Field. In 1982–83 K. Venezia was employed to prepare a floristic inventory of FBF. Andrew Greller did extensive collecting at FBF in 1983 and verified the plants. Lechthaler, Makrinikolas, Risley and Stalter have made limited collections at FBF. Chrysler (1930), McKenian (1968, Master's thesis, Newark State College, Union, New Jersey) and Stalter (1979) have collected plants and prepared floristic inventories of Sandy Hook.

Plants collected at Floyd Bennett Field and Fort Tilden are housed in the herbarium at Floyd Bennett Field. Plants collected at Sandy Hook by Stalter have been placed in the herbaria at Sandy Hook and St. John's University, whereas those collected by Chrysler are in CHRB. Nomenclature generally follows Fernald (1950) or Bailey (1949).

RESULTS AND DISCUSSION

Four hundred and fifty taxa in 80 families have been identifed. The Gramineae (66 species) and Compositae (66 species) are the largest families in the flora. Other families with large numbers of species are: Rosaceae (28 species), Leguminosae (25), Cyperaceae (18), Caryophyllaceae (16), Chenopodiaceae (15), and Cruciferae (14). The largest genera are *Solidago* (9), *Cyperus* (9), and *Juncus* (8). Dominance of herbaceous taxa in the flora is manifest especially at FBF and FT; this study documents the generally graminoid and herbaceous appearance of the landscape.

One hundred sixty-two plants (36 percent) of the Gateway flora are exotics. The Cruciferae (71 percent), Leguminosae (64 percent), and Caryophyllaceae (62.5 percent) contain the greatest percentages of exotics. Twenty-eight grasses (43 percent of the Gramineae) and twenty-three composites (35 percent of the Compositae) are non-native. All eight species of *Trifolium* are introduced. Only one sedge, *Carex kobomugi,* is an alien plant.

The Bayside Holly Forest at Sandy Hook, New Jersey is a unique community in the Gateway National Recreation Area, with *Ilex opaca* Ait. (American Holly) as the dominant species (Stalter, 1979). *Ilex opaca* occurs in all size classes and is well represented in all stages of its life history; these plants are taller and larger in circumference than those of the better known "Sunken Forest" at Fire Island, New York (Art, 1976; Stalter, 1979). However, the oldest American Holly at Sandy Hook is 153 years old (in 1986), whereas

the oldest *Ilex opaca* at Fire Island is 182 years old. Stalter (1979) contended that *Ilex opaca* reaches its best development on the eastern coast at the Bayside Holly Forest.

The rarest plant identified in the present study was *Carex kobomugi* Ohwi, earlier reported by Stalter in 1980. This Asiatic sedge has also been reported at Island Beach State Park, N.J. by Small (1954); in the vicinity of Seaside Park, New Jersey by Michael Canoso (pers. comm.), at two stations in Virginia by Dr. A. M. Harvill (pers. comm.) and three stations in Virginia by Dr. Stewart Ware (pers. comm.). A complete list of species of the Gateway National Recreation Area is available from the senior author upon request.

ACKNOWLEDGMENT

The authors appreciate the assistance of John Tanacredi, Natural Resources Management Specialist at Gateway National Recreation Area, and his co-workers for their support of our research.

LITERATURE CITED

Art, H. W. 1976. Ecological studies of the Sunken Forest, Fire Island National Seashore New York. National Park Service Scientific Monograph Series Number 7, 1976, Washington, D.C.

Bailey, L. H. 1949. Manual of Cultivated Plants. MacMillan. New York.

Chrysler, M. A. 1930. The origin and development of the vegetation of Sandy Hook, New Jersey. Bull. Torrey Bot. Club 57: 163–176.

Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed. American Book Company. New York.

Friedberg, M. P. and Partners. 1980. Floyd Bennett Field Environmental Inventory and Preliminary Land Use Program. Prepared for U.S. National Park Service, Denver Service Center, Denver, CO.

Link, D. A. 1981. Historical structures report archeological data section. Fort Tilden, Gateway National Recreation Area. U.S. National Park Service, Denver Service Center, Denver, CO.

Nordstrom, K. F., J. R. Allen, and N. P. Psuty. 1975. Beach dynamics and sediment mobility of Sandy Hook, New Jersey. Reprinted from Proceedings, Columbia University, on pollution and water resources, Vol. VIII. Special problems on Ocean Engineering, Columbia Univ. Press. New York. Reprint 75–6.

Rogers, G. F., J. M. Robertson, W. D. Solecki, and M. K. Flint. 1985. Rate of *Myrica pensylvanica* (bayberry) expansion in grassland at Gateway National Recreation Area, New York. Bull. Torrey Bot. Club 112: 74 78.

Small, J. A. 1954. *Carex kobomugi* at Island Beach, New Jersey. Ecology 35: 289 291.

Stalter, R. 1979. The plant communities of Sandy Hook, New Jersey with emphasis on *Ilex opaca*. Proceedings of the Second Conference on Scientific Research on the National Parks 11: 26 50.

_____. 1980. *Carex kobomugi* Ohwi at Sandy Hook, New Jersey. Bull. Torrey Bot. Club 107: 431–432.

_____ and LECHTHALER, D. 1984. A floristic study of Fort Tilden, New York. South Carolina Academy of Science XLVI: 126. Abstract.

TANACREDI, J. T. 1983. Coastal zone management practices at an urban National Park. Environmental Management 7: 143–150.

U.S. NATIONAL PARK SERVICE. 1983. Development concept plan and environmental assessment, Floyd Bennett Field, Gateway National Recreation Area. U.S. National Park Service, Denver Service Center, Denver, CO.

R. S.
36 GLADE LANE
LEVITTOWN, NEW YORK 11756

A. G.
DEPARTMENT OF BIOLOGY
QUEENS COLLEGE, CUNY
FLUSHING, NEW YORK 11367

RHODORA, Vol. 90, No. 861, 1988

RANUNCULUS ×SPITZBERGENSIS (NATH.) HADAČ, AN ADDITION TO THE FLORA OF NORTH AMERICA

WILLIAM J. CODY, MARCEL BLONDEAU AND JACQUES CAYOUETTE

ABSTRACT

Ranunculus ×spitzbergensis (Nath.) Hadač, the hybrid between *R. lapponicus* L. and *R. pallasii* Schlecht., is reported for the first time from North America. Four sites in Quebec and one in central District of Keewatin are recorded. Habitats are described, and the characters by which the hybrid may be discerned from the parents are presented. Synonymy is given and the two parents are placed in the same subgenus, *Coptidium*.

Key Words: *Ranunculus lapponicus, R. pallasii, R. ×spitzbergensis, Coptidium,* North America, northern Quebec, central Keewatin

INTRODUCTION

In his paper *Phytogeographical problems in Svalbard,* Rönning (1963) considered *Ranunculus spitzbergensis* Hadač [*Ranunculus ×spitzbergensis* (Nath.) Hadač] endemic to that region. Hadač (1963) echoed that treatment, but transferred the name *spitzbergensis* to the genus *Coptidium* as *C. spitzbergense* (Nath.) Hadač. Hadač (*loc. cit.*, p. 211) wrote: "Spitzbergen, Siberia, Alaska, eastern North America and Greenland have vast areas of never glaciated territories where, by adaptation and isolation during the Ice Age or Ages, new species could be formed, as, for example, *Coptidium spitzbergense, Pedicularis dasyantha, Puccinellia vilfoidea,* etc."

Over 60 years previously, however, Andersson and Hesselman (1900) had illustrated and described in detail a sterile hybrid between the circumpolar species *Ranunculus lapponicus* L. and *R. pallasii* Schlecht., found on the island of Spitzbergen. This hybrid was given the name *R. ×spitzbergensis* (Nath.) Hadač in 1942. Benson (1948), in his treatment of the North American *Ranunculi,* mentioned the existence of the hybrid but did not record its presence in North America. The fact that the putative parents are circumpolar in their distribution would suggest that the hybrid should be found elsewhere, and indeed Bournérias (1971) tentatively identified a specimen from Povungnituk in northern Quebec as this hybrid. Thus, it is not surprising that Tolmatchev (1971) reported it (*sub R. pallasii* var. *minimus* Ruprecht) from five localities in arctic

U.S.S.R. (Kolguyev Island, Yamal Peninsula, Lena River Delta, Uelen Settlement on Bering Strait and Kultushnoe Village at Korf Bay); since then it has been reported from Wrangel Island (Petrovsky, 1973) and the Chukchi Peninsula (Jurtsev et al., 1975; Zaslavskaja et al., 1984).

Of particular interest here is the discovery of *Ranunculus ×spitzbergensis (R. lapponicus × R. pallasii)* from several localities in northern Canada. Data for these collections are as follows:

COLLECTION DATA: **Quebec:** Baie d'Hudson, environs d'Akulivik, 60°48′N, 78°12′W, pré marécageux à *Carex rariflora* et à *Eriophorum angustifolium*, dans les sphaignes, assez abondant mais dispersé, à quelques pas de *R. pallasii, M. Blondeau 85052,* 8 juillet 1985 (QFA, DAO, Herb. Blondeau); *idem,* dans un marais dominé par les mousses et *Potentilla palustris, M. Blondeau 85280,* 16 juillet 1985 (QFA, DAO, Herb. Blondeau); environs d'Ivujivik, 62°24′N, 77°55′W, à la marge d'un ruisseau tranquille, avec *Eriophorum* sp., *M. Blondeau 84278,* 18 juillet 1984 (DAO, QFA); *idem,* petite mare adjacente à un ruisseau, dans les mousses et les cailloux, *M. Blondeau 84248,* 18 juillet 1984 (QFA); Lac Payne, 59°17′N, 73°25′W, rive ouest de la Pointe Ronde, *Legault & Brisson 7971,* 8 août 1965 (CAN, QFA, DAO, SFS); Povungnituk, *M. Bournérias 69251,* 29.VII.1969, (QFA, Herb. Bournérias). **Keewatin:** NW of Imikula Lake, 62°02′N, 97°40′W, single extensive colony among bare boulders in bed of Jaeger Creek and locally in nearby tundra, *K. Reading s.n.,* 17 Aug. 1984 (DAO) (Figure 1).

An examination of *Ranunculus* specimens preserved in the herbaria which house the major collections of plants from northern Canada (CAN, DAO, MTMG, QFA, SFS) did not reveal any collections of the hybrid which had been made by botanists in the past. Most of these individuals, however, did not have the opportunity to study the plants of restricted areas in detail, but rather collected representative specimens as they travelled through the country.

A map of the known distribution of *R. ×spitzbergensis* in northern Quebec and the District of Keewatin is shown as Figure 2.

Hadač (1942, 1944, 1960, 1963), Rönning (1963), and Hultén (1971) considered *Ranunculus ×spitzbergensis* to be a more or less stabilized hybrid between *R. lapponicus* and *R. pallasii,* found in Spitzbergen and Novaya Zemlya. Andersson and Hesselman (1900) described the hybrid between *R. lapponicus* and *R. pallasii* in great detail, comparing it to both putative parents. It was intermediate in many characters between the two and had a very low percentage of stainable pollen. Flovik (1936, 1940) has reported chromosome counts of $2n = 16$ for *R. lapponicus*, $2n = 32$ for *R. pallasii* and $2n = 24$ for the triploid hybrid, *R. ×spitzbergensis,* based on material from Spitzbergen. The occurrence of the hybrid in arctic U.S.S.R.

Figure 1. Specimen of *Ranunculus* ×*spitzbergensis* from Imikula Lake, District of Keewatin (*K. Reading s.n.* DAO).

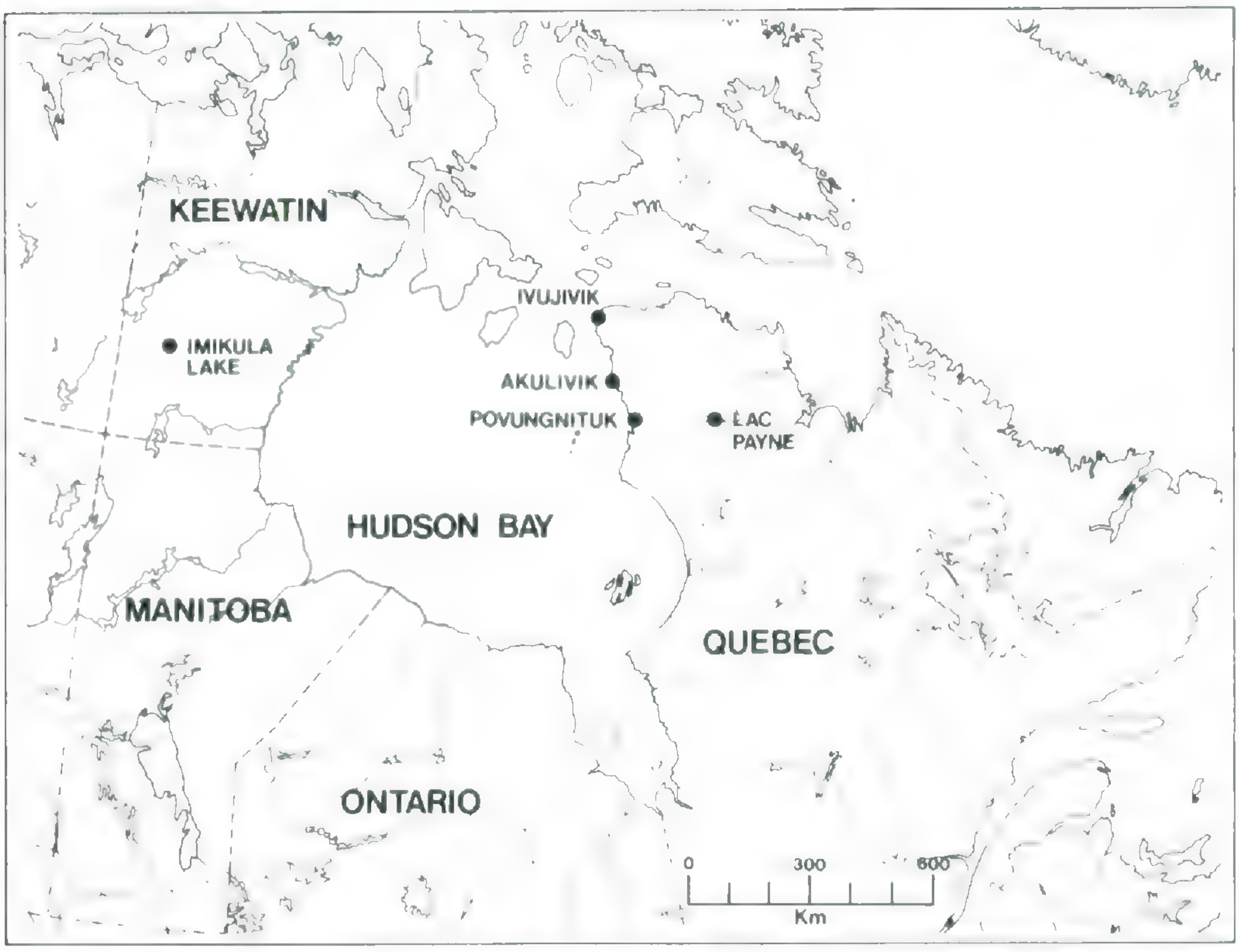


Figure 2. Map of the known distribution of *Ranunculus* ×*spitzbergensis* in northern Quebec and the District of Keewatin.

and particularly in glaciated parts of northern Canada would indicate that the hybridization process has taken place at different times and, indeed, even in Spitzbergen may have occurred several times and not as Hadač (1960) stated: "*Ranunculus spitsbergensis* is perhaps of a hybridogenous origin but certainly not a recent hybrid; it spreads vegetatively only. Its occurrence in several places in Vestspitsbergen, separated by glaciers, and even on Edge Island, could be realized during the last interglacial, not later." Comparative data for *Ranunculus lapponicus, R. pallasii* and *R.* ×*spitzbergensis* based on specimens from the District of Keewatin and northern Quebec are presented in Table 1.

Studies of the pollen of *Ranunculus lapponicus, R. pallasii* and *R.* ×*spitzbergensis* by Andersson and Hesselman (1900) and by the present authors have shown that the pollen of the putative parents has a high percentage of stainability but that of the hybrid has a very low percentage of stainability. Pollen stainability was assessed on Canadian specimens and on one specimen from Svalbard by the lactophenol-cotton blue staining method (Radford et al., 1974) on 100 pollen grains from each sample. In the hybrid, the pollen is of

Table 1. Comparative morphology of *Ranunculus lapponicus*, *R. pallasii* and *R.* ×*spitzbergensis* based on specimens from the District of Keewatin and northern Quebec.

R. pallasii	*R.* ×*spitzbergensis*	*R. lapponicus*
HABITAT AND GROWTH HABIT:		
Marsh or emergent aquatic plants (in small ponds) with creeping or floating freely-branched stems	Similar to *R. pallasii* but less robust, and occurring in very wet *Sphagnum* or at the margins of quiet pools and streams.	Terrestrial, with filiform, creeping stems deeply buried in moss (usually *Sphagnum*)
STEM		
Soft, fistulose, in pressed specimens, (2.5)-3 6 -(7) mm wide	Much like *R. pallasii* but 2 3 mm wide in pressed specimens	Quite fine, 0.7 1.5 mm wide in pressed specimens
PETIOLES OF BASAL LEAVES:		
8 20 cm long, gradually tapering to the bases of the leaves	6 15 cm long, with parallel sides (not tapered)	3 6 cm long, with parallel sides (not tapered)
LEAF BLADE:		
Varying from simple oblong-linear to cuneate with 2 or 3 blunt, upwardly-directed lobes	Lobes 3, oblong-ovate, blunt, wide-spreading, the lower 2 often more or less notched	Deeply 3-lobed, the upper lobe 3- to 5-toothed, the lower lobes 2-lobed and toothed
SEPALS:		
8 10 mm long, ovate	4.5 7.0 long, broadly ovate	3 4 mm long, round
PETALS:		
White; elongate-ovate; 5 to 8 heavy veins	Yellowish-white; broadly ovate; 5 or 6 light veins	Yellow; spathulate; 3 to 5 light veins
STAMENS:		
Ca. 3.5 mm long	2.5 3.5 mm long	Ca. 2.5 mm long

varying sizes, has collapsed walls and is unstained or only faintly stained; such pollen is considered sterile (Table 2).

Ranunculus pallasii is a low arctic species which occurs mainly in the water on the borders of small ponds and streamlets on the tundra, usually but not always near the coast, as noted by Schofield (1959) at Churchill, Manitoba. *Ranunculus lapponicus* is a much more widespread boreal species that extends northward into the tundra regions, where it is usually found in moist sphagnum. Maps of the Canadian distribution of these two species are given in Porsild (1964), Porsild and Cody (1980), and by Rousseau (1974) for

Table 2. Pollen stainability in *Ranunculus lapponicus*, *R. pallasii* and *R.* ×*spitzbergensis* from sites in northeastern Canada and Svalbard.

Species	Locality	Collector & No.; Deposition of Specimen	Pollen Stainability (%)
lapponicus	Akulivik	*Blondeau 85086* (DAO)	97
lapponicus	Imikula Lake	*Reading s.n.* (DAO)	98
pallasii	Akulivik	*Blondeau 85279* (DAO)	94
pallasii	Povungnituk	*Bournérias* 69030 (MTMG)	93
×*spitzbergensis*	Akulivik	*Blondeau 85052* (DAO)	4
×*spitzbergensis*	Akulivik	*Blondeau 85280* (DAO)	2
×*spitzbergensis*	Lac Payne	*Legault & Brisson 7971* (DAO)	15
×*spitzbergensis*	Imikula Lake	*Reading s.n. (a)* (DAO)	0
×*spitzbergensis*	Imikula Lake	*Reading s.n. (b)* (DAO)	0
×*spitzbergensis*	Imikula Lake	*Reading s.n. (c)* (DAO)	2
×*spitzbergensis*	Ivujivik	*Blondeau 84278* (DAO)	0
×*spitzbergensis*	Svalbard	*R. S. Harper R.80* (CAN)	0

Quebec. The hybrid occurs in habitats somewhat similar to those of *R. pallasii* but is more commonly found in wet mosses.

Both the putative parents occur on Spitzbergen (Hultén, 1971), although they may not necessarily now be known from all the localities in which the hybrid is found. Both putative parents are present in arctic U.S.S.R., but it is not known if they are both known from the sites from which the hybrid has been recorded. Petrovsky (1973), however, recorded only *Ranunculus pallasii* from Wrangel Island. For Canadian sites this information is presented in Table 3. The Lac Payne specimen *(Legault & Brisson 7971)* was originally determined as *R. pallasii* and was mapped as that species by Rousseau (1974). Although *R. pallasii* is therefore not known from the Lac Payne area, it is known in Lac Chavigny (Cayouette, 1987) and other sites in the interior of northern Quebec (Rousseau, 1974 — map 444).

Andersson and Hesselman (1900) stated that no fruit, even at the early stages of development, had been observed on the hybrid plants in Spitzbergen. Hadač (1960) stated that the hybrid spreads only vegetatively. This finding is apparently true also for all of the Canadian sites, where again no fruiting specimens have been observed. Figure 3 compares a mature fruiting head of *Ranunculus lapponicus* with an apparently sterile head of *R.* ×*spitzbergensis*.

The site at Jaeger Creek NW of Imikula Lake was observed by Reading (pers. comm.) during the summers of 1983 through 1986.

Table 3. Sites of *Ranunculus* ×*spitzbergensis* in northern Canada from which the putative parents, *R. lapponicus* and *R. pallasii,* are known.

Locality	*R. lapponicus*	*R. pallasii*
Akulivik[1,2]	x	x
Imikula Lake[2]	x	
Lac Payne[2]	x	
Povungnituk[3]	x	x
Ivujivik[1]	x	

[1] *Blondeau* (in prep.)
[2] DAO
[3] *Bournérias (1971)*

Here the colony covers an area of about 25 m by 90 m, with the bulk of the plants in the boulder terrain (which is flooded every spring) and with local incursions into the sphagnum tundra on either side of the creek bed. On 2 July 1986, the shrubby rocky tundra was raised to about 3.5 m above the mid-summer level by an underlayer of ice, so much so that the high and loose boulder beds were unstable to walk on. By mid-summer this terrain had settled into solid beds. The rupturing and tumbling action year after year caused by this ice uplifting may have been a major factor in the vegetative propagation of the hybrid in that area by breaking up the rhizomes and transporting them over short distances. Such observations have not been made at the sites in northern Quebec. There is no evidence of long-distance dispersal of the hybrid. Hybridization seems to have occurred at each locality at some time in the past when such factors as proximity of the parent species, time of flowering, weather, and a suitable habitat for the resulting hybrid were all available at the same time, but this habitat combination has not been evaluated in the present study.

At Akulivik, *Ranunculus* ×*spitzbergensis* grew in wet terrain with *Carex rariflora* (Wahlenb.) Sm. and *Eriophorum angustifolium* Honck. in deep *Sphagnum* moss within about 5 meters of a dense population of *R. pallasii* and on a *Sphagnum* plateau dominated by *Potentilla palustris* (L.) Scop. The hybrid was locally abundant here. At Ivujivik, *R.* ×*spitzbergensis* was found in small pools near brooks and in deep wet mosses. At Povungnituk a sterile plant was found in hummocky *Sphagnum* where *Pinguicula villosa* L. and *Rubus acaulis* Michx. also occurred (M. Bournérias, pers. comm.).

Figure 3. Unfertilized pistils of *Ranunculus* ×*spitzbergensis* (left) and mature fruiting head of *R. lapponicus* (right) photo K. Reading, Imikula Lake, District of Keewatin, mid-August 1984.

The hybrid between *Ranunculus lapponicus* and *R. pallasii* has been treated variously. Synonymy is as follows:

Ranunculus ×**spitsbergensis** (Nath.) Hadač in Stud. Bot. Cechica 5: 3. 1942; Skrifter om Svalbard 87: 36. 1944, *pro sp.*

R. pallasii Schlecht. var. *spetsbergensis* Nath., Kongl. Svensk Vetansk. Akad. Handl. 20: 6. 1883 *sphalm.*

R. lapponicus × *R. pallasii* Andersson and Hesselman, Bidr. Spetsbergens Kärlväxtfl. 42. 1900.

R. pallasii Schlecht. var. *minimus* Ruprecht, Fl. Samojed. Cisur. 18. 1845 [repr. 1846], *fide* Tolmatchev. 1971.

Coptidium spitzbergense (Nath.) Hadač, North Atlantic Biota, 218. 1963.

Benson (1940) divided the North American species of the genus *Ranunculus* into nine subgenera, including *Pallasiantha* L. Benson, (with the monotype, *R. pallasii*) and *Coptidium* (Nym.) L. Benson (with the monotype, *R. lapponicus*). Tutin (1964) pointed out that the previous publications of Beurling and Nyman of *Coptidium* as a subsection were invalid, thus making Prantl's publication of it (1888), although attributed to Beurling, the earliest that can be used. The correct authorities for *Coptidium* as a subgenus should then be

(Prantl) L. Benson, as Benson's reference to Nyman can be considered a bibliographic error of citation (ICBN Art. 33.2). Löve and Löve (1961), in elevating *Coptidium* to the generic level, considered that "Because similarities in size and morphology of the chromosomes, in addition to the morphological characters, seem to indicate a closer relationship between the subgenera *Coptidium* and *Pallasiantha* of Benson, these monotypic groups are kept as subgenera of the same genus for which the former name is legitimate at the generic level." They accordingly made the appropriate transfers for *C. lapponicum* (L.) Löve & Löve and *C. pallasii* (Schlecht.) Löve & Löve. We prefer to treat these species in the genus *Ranunculus,* but agree with Löve & Löve (1961) that because of the close relationship between the two species, they should be in the same subgenus, *Coptidium* (Prantl) L. Benson.

ACKNOWLEDGMENTS

The authors thank Ken Reading for his detailed observations and photographs of the Jaeger Creek stand, John McNeill and Guy Baillargeon for their comments on taxonomy, Marcel Bournérias for information on his collection from Povungnituk, and Clifford Crompton and Gerald Mulligan for their comments on the manuscript.

LITERATURE CITED

Andersson, G. and H. Hesselman. 1900. Bidrag till Kännedomen om Spetbergens och Beeren Eilands Kärlväxtflora. Bihang till Kongl. Svenksa Vetensk. Akad. Handl. Bd. 26. Afd. III. No. 1: 1–88.

Benson, L. 1940. The North American subdivisions of *Ranunculus.* Amer. J. Bot. 27: 799–807.

_____. 1948. A treatise on the North American Ranunculi. Amer. Midl. Nat. 40(1): 1–261.

Bournérias, M. 1971. Observations sur la flore et la végétation des environs de Puvirnituq (Nouveau-Québec). Naturaliste Canad. 98: 216–318.

Cayouette, J. (1987). La flore vasculaire de la région du lac Chavigny (58° 12′N–75° 08′0), Nouveau-Québec. Provancheria, No. 20.

Flovik, K. 1936. The somatic chromosomes of certain arctic species of the genus *Ranunculus.* Commentat. Biol. 5(7): 1–18.

_____. 1940. Chromosome numbers and polyploidy within the flora of Spitzbergen. Hereditas 26: 430–440.

Hadač, E. 1942. Notulae ad floram Svalbardiae spectantes. Stud. Bot. Cech. 5: 1–5.

_____. 1944. Die Gefässpflanzen des "Sassergebietes" Vest-Spitzbergen. Norges Svalbard og Ishavsundersökelser, Skrifter No. 87, 1–71.

_____. 1960. The history of the flora of Spitsbergen and Bear Island and the age of some arctic plant species. Preslia 32: 225–253.

———. 1963. On the History and Age of some Arctic Plant Species, pp. 207–219. *In:* Á. Löve and D. Löve, Eds. North Atlantic Biota and Their History. The Macmillan Co., New York.

Hultén, E. 1971. The Circumpolar Plants. II. Dicotyledons. Kongl. Svenska Vetenskapsakad. Handl. Band 13. Nr. 1.

Jurtzev, B., A. Galanin, T. Derviz-Sokolova, A. Katenin, A. Korobkov, T. Koroleva, V. Petrovsky, T. Plieva, V. Raszhivin and N. Taraskina. 1975. Floristic finds in the Chukchi tundra. Novit. Syst. Pl. Vasc. 12: 301 325.

Löve, Á. and D. Löve. 1961. Some nomenclatural changes in the European flora. I. Species and supraspecific categories. Bot. Not. 114: 33–47.

Petrovsky, V. V. 1973. A list of vascular plants of the Wrangel Island. Bot. Žurn. 58(1): 113–126.

Porsild. A. E. 1964. Illustrated flora of the Canadian arctic archipelago. Natl. Mus. Canada Bull. 146.

——— and W. J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. Natl. Mus. Canada.

Prantl, K. A. E. 1888. *Coptidium. In:* Engler & Prantl, Natur. Pflanzenfam. 3(2): 65.

Radford, A. E., W. C. Dickinson, W. C. Massey and C. R. Bell. 1974. Vascular Plant Systematics. Harper and Row, New York.

Rönning, O. I. 1963. Phytogeographical problems in Svalbard, pp. 99–107. *In:* Á. Löve and D. Löve, Eds., North Atlantic Biota and Their History. The Macmillan Co., New York.

Rousseau, C. 1974. Géographie floristique du Québec –Labrador. Les Presses de l'Université Laval, Québec.

Schofield, W. B. 1959. The salt marsh vegetation of Churchill, Manitoba, and its phytogeographic implications. Natl. Mus. Canada Bull. 160: 107–132.

Tolmatchev, A. I. 1971. *Ranunculus,* pp. 183 225. *In:* A. I. Tolmatchev, Ed., Flora Arctica URSS, Fasc 6, Caryophyllaceae Ranunculaceae. Leningrad.

Tutin, T. G. 1964. *Ranunculus,* p. 54. *In:* Flora Europaea, Notulae Systematicae ad Floram Europaeam spectantes, No. 3. Feddes Repert. Spec. Nov. 69: 1–62.

Zaslavskaja, T., V. Petrovsky and T. Plieva. 1984. Novitates pro flora Czukotka occidentali. Novit. Syst. Pl. Vasc. 21: 221–225.

W. J. C. AND J. C.
BIOSYSTEMATICS RESEARCH CENTRE, AGRICULTURE CANADA
OTTAWA, ONTARIO
CANADA K1A 0C6

M. B.
5010 CLÉMENT-LOCKQUELL
ST-AUGUSTIN, QUEBEC
CANADA G3A 1B3

RHODORA, Vol. 90, No. 861, 1988

TAXONOMIC REVISION OF *VERNONIA* SUBSECT. *CHAMAEDRYS* (COMPOSITAE: VERNONIEAE)

JOHN G. STUTTS

ABSTRACT

Vernonia Schreber subsect. *Chamaedrys* Cabrera consists of sixteen species of woody or suffrutescent perennials from southern South America. The inflorescence is either corymbose-paniculate or thrysoid-paniculate with numerous small- to medium-sized heads containing 4–30 florets. The delimitation of various infrageneric groups in *Vernonia,* as a result of a taxonomic study of *Vernonia* subsect. *Chamaedrys,* is presented. Species excluded from subsect. *Chamaedrys* are transferred to other subgeneric groups. Chemosystematic, palynological and cytological data utilized in the development of a taxonomic revision of *Vernonia* Schreber subsection *Vernonia* Cabrera are presented along with the results of hybridization experiments. A key to the series, subseries and species of *Vernonia* subsect. *Chamaedrys* is given along with descriptions, geographic distributions and ecological information.

Key Words: *Vernonia,* Compositae, Vernonieae, taxonomy, flavonoids, palynology, chromosome numbers, South America

INTRODUCTION

The genus *Vernonia* Schreber has ca. 1,000 species with about one-half of these occurring in the New World. The generic concept of *Vernonia* (Cassini 1817, 1819; Lessing 1829, 1831a, 1831b; de Candolle 1836 and Bentham and Hooker 1873) has remained relatively constant. Infrageneric classifications of *Vernonia,* however, have varied widely (Bentham and Hooker, 1873; Gleason, 1906, 1922; Ekman, 1914; Cabrera, 1944). *Vernonia* exhibits an extreme diversity in vegetative morphological features (Jones, 1976, 1979a; Keeley and Jones, 1979). When combined with parallelism, convergence and reversals in evolutionary trends, this diversity has caused difficulty in circumscribing natural subdivisions and relating these to a workable classification. The most recent attempt to formulate a synoptic classification of *Vernonia* was that of Jones (1979a, 1981a). Jones' classification is an improvement over previous treatments since he treated the genus on a world-wide basis rather than in limited geographic areas as had been done previously (Schultz-Bipontinus, 1861, 1863; Baker, 1873; Cabrera, 1944).

Jones (1979a, 1981a, 1981b) stated that his synoptic classification was a working hypothesis designed to provide workable-sized

groups of species for future taxonomic revisions. The current study of *Vernonia* subsect. *Chamaedrys* Cabrera refines the delimitation of the group as a whole and critically examines species concepts and relationships between groups within the subsection. First recognized by Cabrera (1944), subsect. *Chamaedrys* was treated as consisting of two species, *Vernonia chamaedrys* Less. and *V. cupularis* Chodat. The subsection was enlarged by Jones (1979a) to include 24 species, not including *Vernonia cupularis*. Some of the species included by Jones have been excluded and other species added to the subsection in Part I of this study resulting in new infrasubsectional classification of the group. Part II presents information which was used to verify species alignments which are presented in Part III. Part III also provides a key to the various series, subseries and species of subsect. *Chamaedrys* and includes descriptions, geographic distributions, and available ecological and phenological information.

Subsect. *Chamaedrys* is a group of woody or suffrutescent perennials centered in the states of Paraná and São Paulo, Brazil but distributed from northern Argentina north to the states of Goiás and Bahia in Brazil, and from there westward to Paraguay and southern Bolivia. As with many Compositae genera, it is difficult to delimit the morphological characters of the infrageneric groups in such a way that they are mutually exclusive. However these groups (i.e., sections and subsections) do have certain combinations of morphological characters which make them recognizable. The species forming the central core of subsect. *Chamaedrys* (i.e., those in series *Chamaedrys*) form an easily recognizable group but some of the peripheral species (i.e., those in series *Nitidulae* and series *Nudiflorae*) tend to approach other subsections of *Vernonia* in certain morphological characters. In this subsection, the heads are generally numerous, small to medium-sized, and contain 4–30 florets. The phyllaries often extend down the pedicel for some distance giving the heads an elongated appearance. This elongation is often greatly exaggerated in specimens infested by insect larvae or fungi, first noted by A. C. P. de Candolle (1814) and confirmed by personal observation. The inflorescence is either corymbose-paniculate or thyrsoid-paniculate. Except for series *Nitidulae*, the species have a xylopodium, an enlarged underground woody base from which the stems and roots grow. New stems may arise directly from the xylopodium, but they usually arise from buds near the bases of older stems which have died back nearly to the base. The species in this subsection are typically found in campo or cerrado habitats and in

open or disturbed sites in the Brazilian Atlantic forest zone (*sensu* Eiten, 1972). Only *V. nitidula* Less. occurs in the coastal forest (i.e., the *mata pluvial da en costa atlantica* of Cabrera and Klein, 1980). Most of the species in subsect. *Chamaedrys* are adapted to areas of seasonal drought or areas which naturally burn over fairly regularly. Much of the above-ground portions of these plants will die back during periods of severe stress and then grow new stems once conditions become more favorable. Species in series *Nitidulae* do not die back regularly. Foliage in subsect. *Chamaedrys* is variable in appearance.

Field work is absolutely essential in order to develop a good understanding of species concepts in *Vernonia,* and it would have been impossible to analyze accurately species relationships within subsect. *Chamaedrys* without first-hand field knowledge of critical taxa. Species of subsect. *Chamaedrys* were observed and collected in the states of Santa Catarina, Paraná, São Paulo, Minas Gerais and Goiás, Brazil, during 1980 and 1982. The herbarium specimens and live plant material collected on these field trips have greatly supplemented the previously available materials.

The taxonomic treatment presented here is the result of the synthesis of several systematic approaches including chemosystematics, cytology, palynology and traditional herbarium techniques. Herbaria from which specimens were borrowed are listed in the acknowledgments. The chemosystematic data indicate that the group forms a cohesive unit. This information is presented in Part II along with the results of the cytological, palynological and hybridization studies.

A study of morphological features was made for each species. Some characters such as inflorescence type and number of florets per head were useful in delimiting species and species groups (i.e., series and subseries). Other characters such as number of pappus bristles and corolla length generally overlapped or were too variable to be useful in the classification. Some characters, including leaf shape and size, were highly variable in some species but fairly constant in others. Leaf sizes are those for middle to lower stem leaves unless otherwise indicated. Some of the species in subsect. *Chamaedrys,* such as *Vernonia oligactoides* Less., are easily defined morphologically and are fairly uniform throughout their ranges. Other species, such as *V. nitidula,* exhibit phenotypic plasticity, especially in vegetative characters but also in reproductive or reproductively related characters such as involucral size, number of

florets per head and pappus color. This variability appears to be similar to the situations found in *Vernonia* sect. *Stengelia* (Schultz-Bip. ex Walp.) Benth. and Hook. (Smith, 1971) and in *Pollalesta* H.B.K. (Stutts, 1981).

PART I:
EXCLUSIONS AND NEW INFRAGENERIC TAXA

SPECIES EXCLUDED FROM SUBSECT. *CHAMAEDRYS*

The following species included in subsect. *Chamaedrys* by Jones (1979a) and others are now excluded from the subsection: *Vernonia jalcana* Cuatrec., *V. puberula* Less., *V. quinqueflora* Less., *V. myrsinites* E. Ekman, *V. pycnostachya* DC., *V. rosea* C. Martius ex DC. and *V. vepretorum* C. Martius ex DC. The morphological and chemical bases for the removal of these species from subsect. *Chamaedrys* are discussed in Part II of this paper. *Vernonia jalcana* is transferred back to subsect. *Eremosis* (DC.) S. Jones where it was originally placed by Cuatrecasas (1965). *Vernonia quinqueflora* and *V. puberula* are assigned to a new series, *Puberulae,* in subsect. *Polyanthes* E. Ekman. The other excluded species are placed in the new series *Tomentellae* in subsect. *Brevifoliae* Cabrera.

REDELIMITATION OF SUBSECT. *NUDIFLORAE* CABRERA

As treated by Jones (1979a), subsect. *Nudiflorae* Cabrera consists of four series: series *Nudiflorae* S. Jones, series *Brevifoliae* (Cabrera) S. Jones, series *Verbascifoliae* S. Jones and series *Subulatae* S. Jones. Series *Buddleiifoliae* is the correct name for the series originally named series *Verbascifoliae* S. Jones (Jones, 1982). The type species for series *Nudiflorae, Vernonia nudiflora* Less., herein is transferred to subsect. *Chamaedrys.* This necessitates a new name for subsect. *Nudiflorae* Cabrera sensu Jones (1979a) and a redelimitation of series *Nudiflorae* S. Jones. At present the three series not affected by these changes are retained in one subsection. This retention is done by reinstating series *Brevifoliae* (Cabrera) S. Jones to its original rank as a subsection and expanding it to include series *Brevifoliae, Buddleiifoliae* and *Subulatae* plus a new series, series *Tomentellae,* as follows:

Vernonia subsect. **Brevifoliae** Cabrera. Darwiniana 6: 303. 1944.
TYPE SPECIES: *Vernonia brevifoliae* Less.

Herbaceous perennials, sometimes woody at the base, or rarely annuals; leaves linear to lanceolate to ovate to oblanceolate; inflorescence corymbose-paniculate or reduced to a simple raceme or spike, or rarely solitary heads; heads with 10–80 florets.

This subsection includes series *Brevifoliae,* series *Buddleiifoliae,* series *Subulatae* and the new series, series *Tomentellae.*

Vernonia series **Tomentellae** Stutts, *ser. nov.*

Frutices vel suffrutices; folia linearia vel ovata vel oblanceolata; inflorescentiae racemi vel spicae vel paniculae erectae; capitula mediocria vel magna, 20–60 flosculis. TYPE SPECIES: *Vernonia tomentella* C. Martius ex DC.

Fruticose or suffrutescent perennials; leaves linear to ovate to oblanceolate; inflorescences racemes or spikes or paniculate, erect; heads medium to large in size, with 20–60 florets.

The following species are included in series *Tomentellae: Vernonia foliosa* Gardner, *V. myrsinites* E. Ekman, *V. pycnostachya* DC., *V. rosea* C. Martius ex DC., *V. rosmarinifolia* Less., *V. tomentella* C. Martius ex DC. and *V. vepretorum* C. Martius ex DC. This group is recognized at the series level within subsect. *Brevifoliae* rather than treated as a separate subsection. A thorough study of the entire subsection will be necessary to delimit clearly the relationships between these series. Some of the species assigned to series *Tomentellae,* such as *Vernonia foliosa* and *V. rosmarinifolia,* may have closer affinities to other species and may have to be removed from this series at a later date. In this case, where some affinity seems to exist, it seems better to include these species in series *Tomentellae* than not to place them in any subgeneric group.

Series *Nudiflorae,* as recognized by Jones (1979a), must be split. One portion remains as a redelimited series *Nudiflorae* (defined later in this paper) and is assigned to subsect. *Chamaedrys.* A second group of species is removed and treated as a new series in subsection *Polyanthes* E. Ekman.

Vernonia series **Brasilianae** Stutts, *ser. nov.*

Herbae perennes vel suffrutices; caules simplices vel raro ramosi; folia lanceolate vel elliptica vel oblanceolata; inflorescentiae corymboso-paniculatae; capitula 10–25 flosculis. TYPE SPECIES: *Vernonia brasiliana* (L.) Druce.

Herbaceous or suffrutescent perennials; stems simple or rarely branched; leaves lanceolate to elliptic or oblanceolate; inflorescence corymbose-paniculate; heads with 10–25 florets.

Series *Brasilianae* is assigned to subsect. *Polyanthes* E. Ekman and contains the following species: *Vernonia brasiliana* (L.) Druce, *V. mariana* C. Martius, *V. scabra* Pers. and *V. tweediana* Baker. Subsection *Polyanthes* needs to be critically examined in order to determine relationships between species groups currently assigned to it.

The following species included in series *Nudiflorae* by Jones (1979a) are excluded for the present time from either series *Brasilianae* or the redefined series *Nudiflorae: Vernonia amplexicaulis* Fries., *V. amygdalina* Lam., *V. densiflora* Gardner, *V. echioides* Less., *V. incana* Less., *V. lorentensis* Hieron., *V. missionis* Gardner, *V. pseudo-linearifolia* Hieron., *V. scapagera* Baker and *V. westiniana* Less. While some of these species may belong in either series *Brasilianae* or series *Nudiflorae*, not enough information is available to place them in an infrageneric taxon at this time. These species should be examined in conjunction with a study of subsect. *Brevifoliae* as delimited in this treatment.

DELIMITATION OF SUBSECT. *CHAMAEDRYS*

Subsect. *Chamaedrys* was first recognized by Cabrera (1944) and was later expanded by Jones (1979a). Subsection *Chamaedrys* is hereby redelimited as follows to include series *Nitidulae*, series *Chamaedrys* (including subseries *Chamaedrys* and subseries *Laxae*) and series *Nudiflorae* (including subseries *Nudiflorae* and subseries *Chaquenses*).

Vernonia subsection **Chamaedrys** Cabrera, Darwiniana 6: 307. 1944. TYPE SPECIES: *Vernonia chamaedrys* Less.

Fruticose to suffrutescent perennials with a xylopodium or shrubs without a xylopodium; inflorescence thyrsoid-paniculate or corymbose-paniculate; heads small to medium sized, generally numerous, with 4–30 florets; involucres turbinate to campanulate, the phyllaries imbricate in several series.

The species included in subsect. *Chamaedrys* are listed under the appropriate series and subseries below.

Vernonia series **Nitidulae** (Cabrera) Stutts, *stat. nov.*

Vernonia subsect. *Nitidulae* Cabrera, Darwiniana 6: 347. 1944. TYPE SPECIES: *Vernonia nitidula* Less.

Shrubs without a xylopodium, generally having several highly branched stems; leaves elliptic to ovate, occasionally linear to

oblanceolate; inflorescence corymbose-paniculate, heads numerous, with 5–30 florets.

The following species are included in series *Nitidulae: Vernonia crassa* (Vell. Conc.) E. Ekman ex Malme, *V. nitidula* Less. and *V. squamulosa* Hook. & Arn.

Vernonia series **Chamaedrys**

Frutices vel suffrutices cum xylopodiis; caules simplices vel raro ramosi infra inflorescentias; folia linearia vel ovata vel oblanceolata; inflorescentiae thyrsoideo-paniculatae; capitula numerosa sessilia vel breve pedicellata, 4–25 flosculis. TYPE SPECIES: *Vernonia chamaedrys* Less.

Fruticose or suffrutescent perennials with a xylopodium; stems one to several from the xylopodium, generally not highly branched below the inflorescence; leaves linear to ovate to oblanceolate; inflorescence thyrsoid-paniculate; heads with 4–25 florets, numerous, sessile to very short pedicellate; involucres turbinate to approaching campanulate.

Series *Chamaedrys* is treated as consisting of two subseries and its constituent species are listed below under the appropriate subseries.

Vernonia subseries **Chamaedrys**

Frutices vel suffrutices cum xylopodiis; inflorescentiae dense thyrsoideo-paniculatae; capitula sessilia vel breve pedicellata, 4–25 flosculis. TYPE SPECIES: *Vernonia chamaedrys* Less.

Fruticose or suffrutescent perennials with a xylopodium; inflorescence densely thyrsoid-paniculate; heads sessile or very short pedicellate with 4–25 florets. Otherwise having the general characters of the series.

The following species are included in subser. *Chamaedrys: Vernonia chamaedrys* Less., *V. cuneifolia* Gardner, *V. mucronulata* Less., *V. oligactoides* Less. and *V. oligolepis* Schultz-Bip. ex Baker.

Vernonia subseries **Laxae** Stutts, *subser. nov.*

Frutices vel suffrutices cum xylopodiis; inflorescentiae laxe thyrsoideo-paniculatae; capitula sessilia vel breve pedicellata, 10–15 flosculis. TYPE SPECIES; *Vernonia laxa* Gardner.

Fruticose or suffrutescent perennials with a xylopodium; inflorescence laxly thyrsoid-paniculate; heads sessile or short pedicellate with 10–15 florets. Otherwise having the general characters of the series.

The following species are included in subser. *Laxae: Vernonia elsieae* Stutts (1983), *V. laxa* Gardner and *V. viscidula* Less. Subseries *Laxae* is assigned to series *Chamaedrys*.

Vernonia series **Nudiflorae** S. Jones p.p. (emend. Stutts)

Vernonia series *Nudiflorae* S. Jones, Rhodora 81: 437. 1979. TYPE SPECIES: *Vernonia nudiflora* Less.

Fruticose or suffrutescent perennials with a xylopodium; stems one to several from the xylopodium, generally not branched below the inflorescence; inflorescence corymbose-paniculate; heads several to numerous, pedicellate, with 10–30 florets; involucre campanulate to approaching turbinate.

Series *Nudiflorae* is treated as consisting of two subseries and its constituent species are listed below under the appropriate subseries.

Vernonia subseries **Nudiflorae**

Frutices vel suffrutices cum xylopodiis; folia linearia vel lineari-lanceolata; inflorescentiae corymboso-paniculatae; capitula 10–20 flosculis. TYPE SPECIES: *Vernonia nudiflora* Less.

Fruticose or suffrutescent perennials with a xylopodium; leaves linear or linear-lanceolate; inflorescence corymbose-paniculate; heads with 10–20 florets. Otherwise having the general characters of the series.

The following species are included in subser. *Nudiflorae: Vernonia lucida* Less. and *V. nudiflora* Less.

Vernonia subseries **Chaquenses** Stutts, *subser. nov.*

Suffrutices cum xylopodiis; folia anguste oblanceolata vel elliptica; inflorescentiae corymboso-paniculatae; capitula 10–30 flosculis. TYPE SPECIES: *Vernonia chaquensis* Cabrera.

Suffrutescent perennials with a xylopodium; leaves narrowly oblanceolate to elliptic; inflorescence corymbose-paniculate; heads with 10–30 florets. Otherwise having the general characters of the series.

The following species are included in subser. *Chaquenses: Vernonia chaquensis* Cabrera, *V. cuplularis* Chodat and *V. schulziana* Cabrera. Subseries *Chaquenses* is assigned to series *Nudiflorae*.

ESTABLISHMENT OF SERIES *PUBERULAE*

Some of the species excluded from subsect. *Chamaedrys* are small trees which seem to be related to certain species currently assigned to subsect. *Polyanthes*. This group of species is treated as a new series as follows:

Vernonia series **Puberulae** Stutts, *ser. nov.*

Arbusculae; folia lanceolata vel elliptica; inflorescentiae paniculatae vel cymoso-semiscorpioideae; capitula parva, 5 20 flosculis; phyllaria parva. TYPE SPECIES: *Vernonia puberula* Less.

Small trees; leaves lanceolate to elliptic; inflorescence paniculate to semiscorpioid-cymose; heads small, with 5–20 florets; phyllaries small.

Series *Puberulae* is assigned to subsect. *Polyanthes* E. Ekman and contains the following species: *Vernonia discolor* Less., *V. oppositifolia* Less., *V. puberula* Less., and *V. quinqueflora* Less. A thorough study of subsect. *Polyanthes* is needed. Some of the species included here were treated by Cabrera & Klein (1980) as belonging to sect. *Critoniopsis* (Schultz-Bip.) Benth. & Hook. [= subsect. *Eremosis* (DC.) S. Jones]. Table 1 presents a summary of past and presently-proposed alignments of subsect. *Chamaedrys*.

PART II.
CHEMOSYSTEMATICS, PALYNOLOGY, CYTOLOGY, AND HYBRIDIZATION

Susquiterpene Lactone Survey

Leaves of nine of the sixteen species of the subsection were tested for the presence of sesquiterpene lactones, including at least one species from each series. The species surveyed for sesquiterpene lactones were *Vernonia crassa, V. nitidula, V. chamaedrys, V. mucronulata, V. oligolepis, V. laxa* and *V. nudiflora* (Table 2). Voucher specimens of each collection sampled are on deposit at GA. Testing procedures used were those of Yoshioka, et al. (1973). The sesquiterpene extracts were chromatographed on 20 × 20 cm thin layer plates of silica gel-G with 0.3 M KH_2PO_4 buffer. Plates were develped in two dimensions, first in chloroform: petroleum ether (4:1) and secondly in chloroform: benzene (1:1). Developed plates were sprayed with a reagent consisting of 0.5 gm vanillin dissolved in 9 ml 95% ethanol, 0.5 ml concentrated sulfuric acid and three drops concentrated acetic acid (Picman et al., 1980).

All species tested exhibited similar spot patterns and color reactions. The three collections of *Vernonia nitidula* tested exhibited slight variation in their spot patterns. No attempt was made to identify the sesquiterpene compounds. The species of subsection *Chamaedrys* appear to contain similar sesquiterpene lactones but structural analysis of these compounds is needed to confirm this assumption.

Table 1. Outline of previous and present classifications[a]

Previous Scheme[b]	Present Scheme
Subsect. *Chamaedrys* Cabrera	Subsect. *Chamaedrys* Cabrera
Vernonia chamaedrys Less.	Series *Nitidulae* (Cabrera) Stutts
V. chaquensis Cabrera	*V. crassa* (Vell. Conc.) E. Ekman ex Malme
V. crassa (Vell. Conc.) E. Ekman ex Malme	*V. nitidula* Less.
V. cuneifolia Gardner	*V. squamulosa* Hook. et Arn.
V. elsieae Stutts[c]	Series *Chamaedrys* Stutts
V. jalcana Cuatrec.	Subseries *Laxae* Stutts
V. laxa Gardner	*V. elsieae* Stutts
V. mucronulata Less.	*V. laxa* Gardner
V. myrsinites E. Ekman	*V. viscidula* Less.
V. nitidula Less.	Subseries *Chamaedrys* Stutts
V. oligactoides Less.	*V. chamaedrys* Less.
V. oligolepis Schultz-Bip. ex Baker	*V. cuneifolia* Gardner
V. puberula Less.	*V. mucronulata* Less.
V. pycnostachya DC.	*V. oligactoides* Less.
V. quinqueflora Less.	*V. oligolepis* Schultz-Bip. ex Baker
V. rosea C. Martius ex DC.	Series *Nudiflorae* S. Jones emend. Stutts
V. squamulosa Hook. et Arn.	Subseries *Nudiflorae* Stutts
V. tomentella C. Martius ex DC.	*V. lucida* Less.[d]
V. vepretorum C. Martius ex DC.	*V. nudiflora* Less.
V. viscidula Less.	Subseries *Chaquenses* Stutts
Subsect. *Nudiflora* Cabrera	*V. chaquensis* Cabrera
Series *Nudiflorae* S. Jones	*V. cupularis* Chodat[d]
V. brasiliana (L.) Druce	*V. schulziana* Cabrera[d]
V. mariana C. Martius	Subsect. *Brevifoliae* Cabrera
V. nudiflora Less.	Series *Tomentellae* Stutts
V. scabra Pers.	*V. foliosa* Gardner[d]
V. tweediana Baker	*V. myrsinites* E. Ekman
Subsect. *Polyanthes* E. Ekman	*V. pycnostachya* DC.
V. discolor Less.	*V. rosea* C. Martius ex DC.
V. oppositifolia Less.	*V. rosmarinifolia* Less.[d]
	V. tomentella C. Martius ex DC.
	V. vepretorum C. Martius ex DC.
	Subsect. *Polyanthes* E. Ekman
	Series *Brasilianae* Stutts
	V. brasiliana (L.) Druce
	V. mariana C. Martius
	V. scabra Pers.
	V. tweediana Baker
	Series *Puberulae* Stutts
	V. discolor Less.
	V. oppositifolia Less.
	V. puberula Less.
	V. quinqueflora Less.

Table 1. Continued.

Previous Scheme[b]	Present Scheme
	Subsect. *Eremosis* (DC.) S. Jones
	V. jalcana Cuatrec.

a. Only those species considered in this paper are listed and some groups do contain other species. b. sensu Jones (1979). c. as *V. rigiophylla* Schultz-Bip. ex Baker. d. not treated by Jones (1979).

Flavonoid Survey

A survey of the leaf flavonoids of each species of the subsection was carried out by a combination of paper, column and thin layer chromatography utilizing the methods of Giannasi (1975). Collections sampled for their flavonoid constituents are listed in Table 3. Figure 1 shows the relative positions of each compound on two-dimensional paper chromatograms. The major compounds identified were flavone aglycones, apigenin-C-glycosides, and quercetin and apigenin-7-O-glycosides. Twenty eight flavonoids were completely or partially identified while several other glycosides were present in various species in concentrations too low to be identified. A total of 40 compounds was detected as discrete spots on paper chromatograms. Table 4 gives the pertinent spectral, R_f and color reaction data and tentative identities for the individual flavonoids. The flavonoid distributions given for each species in Table 5 (presence or absence of compounds) represent a composite of all samples tested for each taxon.

Twelve of the compounds elucidated are O-glycosides including nine quercetin-O-glycosides and three apigenin-O-glycosides. One of the apigenin-O-glycosides, compound 3C, gave unusual spectral data. By its R_f values the compound seems to be a glycoside and it yields the aglycone apigenin upon acid hydrolysis. However, the original ultraviolet spectrum of the compound also looks like apigenin aglycone, i.e., sugars appear to be absent. These conflicting results certainly invite further study. This compound was detected only in *Vernonia crassa*. The two other apigenin-O-glycosides, compounds 3A and 3B, were difficult to separate on two-dimensional paper chromatograms but could be separated on polyamide TLC plates developed in methyl-ethyl ketone solvent or on paper using distilled water. Many of the leaf samples used were small and since compound 3B (apigenin-7-O-diglucoside) is normally present in much lower concentration than compound 3A (apigenin-7-O-glycoglucoside), it may have been present in other species than those indicated and simply was not detected.

Table 2. Collections of *Vernonia* subsect. *Chamaedrys* tested for the presence of sesquiterpene lactones.

V. crassa (Vell. Conc.) E. Ekman ex Malme
BRAZIL: Paraná, Mun. Balsa Nova, São Louis do Puruna, *Stutts 1008*.

V. nitidula Less.
BRAZIL: São Paulo, Serra da Bociana, São Jose da Barrareiro, *Stutts 848*, *Stutts 851*. Paraná, Mun. Curitiba, BR 376, km 37, *Stutts 1004*.

V. chamaedrys Less.
BRAZIL: Paraná, BR 277. 28 km W of Guarapuava, *Stutts 1227*.

V. mucronulata Less.
BRAZIL: Paraná, Mun. do Jaguariaiva, estrada do Arapoti, *Stutts 1200*.

V. oligolepis Schultz-Bip. ex Baker
BRAZIL: Paraná, Mun. Ponta Grossa, Rio Tibagi, BR 376, *Stutts 1178*.

V. laxa Gardner
BRAZIL: Minas Gerais, Serra de Espinacho, ca 15 km NE of Diamantina, *Stutts 935*.

V. nudiflora Less.
BRAZIL: Paraná, Mun. Ponta Grossa, Rio Tibagi, BR 376, *Stutts 1180*.

Five of the compounds are apigenin-6, 8-C-diglycosides, three of which also have O-glycosyl sugars at the 7 position (compounds 6, 6C and 11) and one of which has xylose as an O-glycosyl sugar attached to the C-glycosyl sugars at both the six and eight positions (compound 4). Two of these C-glycosides, compounds 4 and 11, seem to have identical C-glycosyl sugars at the 6 and 8 positions as indicated by a lack of formation of isomers during boiling in acid solution. The other three C-glycosides seem to have different sugars at the 6 and 8 positions. Compound 6 yields compound 5 upon acid hydrolysis by removal of the sugar from the 7 position. This sugar could not be hydrolized by glucosidase, suggesting that it is not glucose.

The other compounds include six flavone aglycones, two flavonol aglycones and three flavanones. The three flavanones, compounds 13, 14 and 28, all appear to be glycosides with compound 14 having glucose at either the 3′ or 4′ position and compound 28 (found only in hybrids) having an undetermined sugar at the 7 position. Compound 13 is glycosylated at an undetermined location. No luteolin-glycosides or kaempferol compounds were detected.

The species of series *Chamaedrys* subseries *Chamaedrys* tend not to produce flavonol-3-O-glycosides (two of the five species produce one) and the species of series *Nudiflorae* subseries *Nudiflorae*

Table 3. Collections of *Vernonia* subsect. *Chamaedrys* analyzed for their flavonoid constituents.

V. chamaedrys Less.

BRAZIL: Mato Grosso do Sul, *D. Sucre 10577;* Paraná, *Stutts 1289, Stutts 1227.* PARAGUAY: Guaira, *Iamo 5414.* ARGENTINA: Misiones, *Schwarz 5471, Medina 275, Meorite 698, Schwarz 669;* Chaco, *Parodi 8521, Buratovich 844;* Corrientes, *Huidobro 4701;* Formosa, *Ismael Morel 189.*

V. chaquensis Cabrera

ARGENTINA: Chaco, *A. G. Schulz 968;* Corrientes, *T. M. Pedersen 1708.*

V. crassa (Vell. Conc.) E. Ekman ex Malme

BRAZIL: Paraná, *Stutts 1008, Stutts 1192, P. Dusen & Jonsson 209a, Dziewa 37, A. P. Duarte 5377, Hatschbach 8107, Hatschbach 19881, Hatschbach 22103, Labouriau 1086.*

V. cuneifolia Gardner

BRAZIL: Mato Grosso do Sul, *Veloso s.n.;* Minas Gerais, *Magalhaes 2876.* PARAGUAY: Amambay, *Hassler 10464, Hassler 11850, P. Jorgensen 4431.*

V. cupularis Chodat

ARGENTINA: Missiones, *Montes 550, Montes 1998;* Corrientes, *T. M. Pedersen 2625.*

V. elsieae Stutts

BRAZIL: Goias, *Riedel s.n.*

V. laxa Gardner

BRAZIL: Minas Gerais, *Stutts 935, E. Pereira 1692.*

V. lucida Less.

BRAZIL: Minas Gerais, *A. P. Duarte 2003, Magalhaes s.n., H. S. Irwin et al. 20508.*

V. mucronulata Less.

BRAZIL: Minas Gerais, *Lito 1808, L. O. Williams & V. Assis 8025;* São Paulo, *Hoehne 2218, Hoehne 2239;* Paraná, *P. Dusen 14125, Stutts 1015, Stutts 1200.*

V. nitidula Less.

BRAZIL: Minas Gerais, *E. Pereira 9162, A. C. Brade 17046, A. F. Regnell I-206, Soares Nunes s.n.;* São Paulo, *A. C. Brade 21177, E. Pereira 5945, Hoehne 3955, Stutts 845, Stutts 846, Stutts 847, Stutts 848, Stutts 849, Stutts 850, Stutts 851;* Paraná, *Hatschbach 774, Stutts 1004, Moreira 322, J. L. Lindeman & J. H. Haas 2655, Hatschbach 22774, Hatschbach 22424, Hatschbach 17304, P. Dusen 10329;* Santa Catarina, *A. P. Duarte 3152, L. B. Smith et al. 7645.* PARAGUAY: *P. Jorgensen 4430,* Guaira, *Montes 12719.* ARGENTINA: Entre Ríos, *Burkart & Troncoso 28089, Cabrera 1937;* Misiones, *Schwarz 1344;* Chaco, *T. Rojas 12191.* URUGUAY: Lavalleja, *Del Puerto 2275;* Artigas, *G. Herter 485 B.*

V. nudiflora Less.

BRAZIL: Paraná, *Stutts 1180, Stutts 1283, S. Jones 22708.*

V. oligactoides Less.

BRAZIL: São Paulo, *A. C. Brade 16201, H. F. L. Filho 760, A. C. Brade 15696;* Paraná, *Stutts 1198, P. Dusen 9626, P. Dusen 9680.* PARAGUAY: Amambay, *T. Rojas 10186.*

Table 3. Continued.

V. oligolepis Schultz-Bip. ex Baker
BRAZIL: São Paulo, *S. M. de Campos 172;* Paraná, *A. C. Brade 19546, P. Dusen 9192, Stutts 1178, Stutts 1199, S. Jones 22718, S. Jones 22711, S. Jones 22729.*

V. schulziana Cabrera
ARGENTINA: Chaco, *A. G. Schulz 3757.*

V. squamulosa Hook. & Arn.
BOLIVIA: Camiri, *W. M. A. Brooke 5578;* Rosal, *W. M. A. Brooke 5713.*
ARGENTINA: Catamarca, *P. Jorgensen 1000;* Tucuman, *S. Venturi 2559;* Jujuy, *Cabrera 4539.*

V. viscidula Less.
BRAZIL: Minas Gerais, *L. O. Williams & V. Assis 6592, L. O. Williams & V. Assis 7139, Roth 1616, A. P. Duarte 8103.*

HYBRIDS

V. chamaedrys × *V. nudiflora*
Greenhouse cross of *Stutts 1289* × *Stutts 1180.*

V. crassa × *V. nitidula*
BRAZIL: Paraná, *Stutts 1010.*

V. crassa × *V. nudiflora*
BRAZIL: Paraná, *P. Dusen 14831, P. Dusen & Jonsson 200a.*

V. oligolepis × *V. oligactoides*
BRAZIL: Paraná, *Stutts 1204.*

V. oligolepis × *V. nudiflora*
BRAZIL: Paraná, *R. Reiss 43 A, Stutts 1280.*

apparently lack flavanones. Aside from this discovery, the distribution of flavonoids was fairly homogenous among the species tested with no major differences between the various series or subseries.

The six putative natural hybrids and one synthetic hybrid tested showed patterns similar to those of their parental species, although on the average the hybrids tended to produce fewer aglycones and an equal or larger number of glycosides than the individual parental species (Table 5). Compounds were often present in higher concentrations in hybrids than in parental species. This was determined by extracting the flavonoids from equal amounts of leaf material of parentals and hybrids, redissolving the flavonoids in equal amounts of methanol, chromatographing equal amounts of the dissolved extract on two-dimensional paper chromatograms, and observing the relative amounts of flavonoids present. The one synthetic hybrid (*Vernonia chamaedrys* × *V. nudiflora*) produced all eight of the

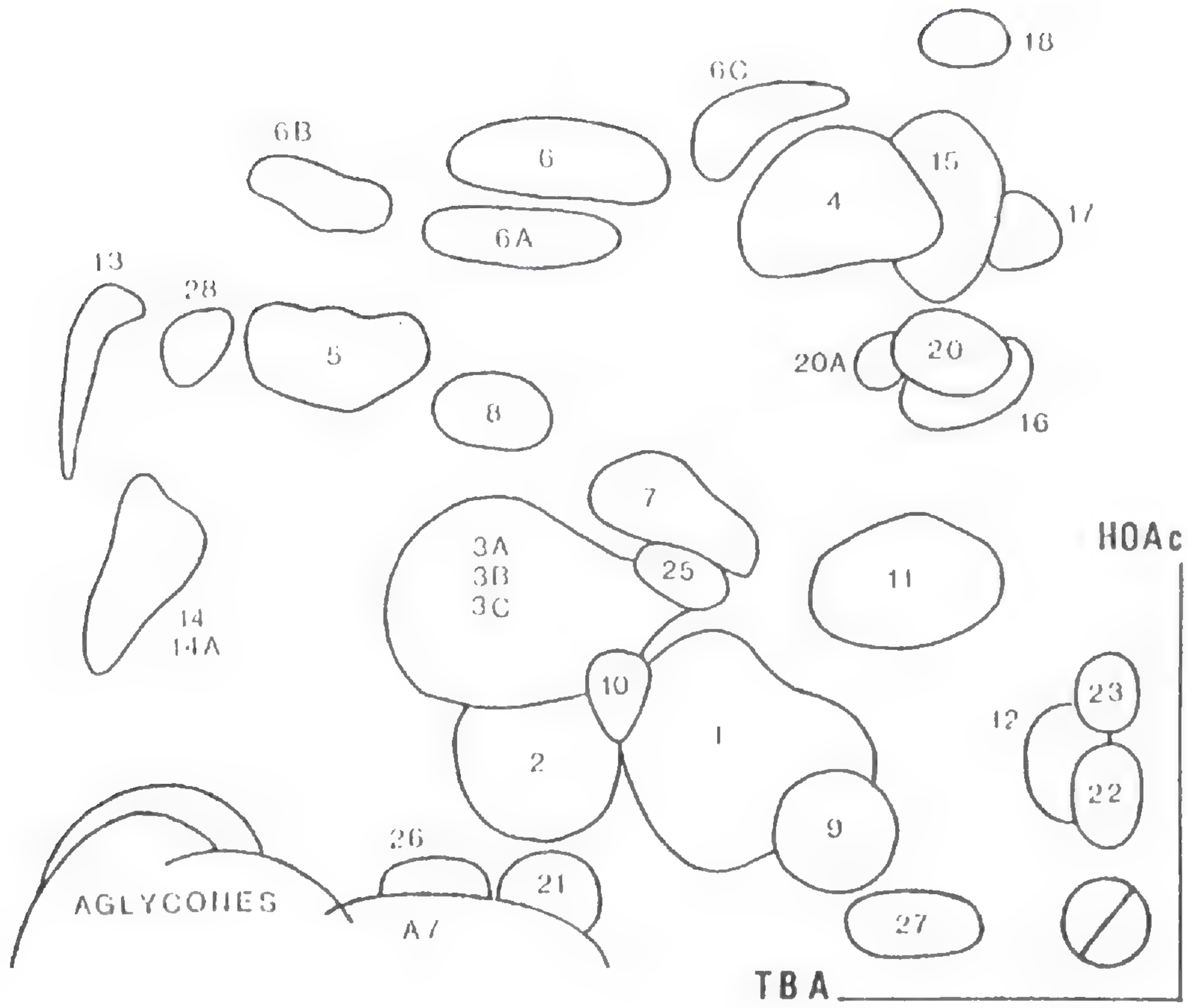


Figure 1. Composite chromatograph of flavonoids of *Vernonia* subsect. *Chamaedrys*.

aglycones and sixteen of the twenty glycosides identified in the study including a flavone-glycoside (compound 3B) and a flavanone-glycoside (compound 28) not detected in either parent. Compound 28 was found in five of the seven hybrids but was not detected in any of the species.

Both qualitative and quantitative variations in flavonoid production were observed in several species including *Vernonia chamaedrys, V. viscidula, V. mucronulata* and particularly *V. nitidula* and *V. nudiflora*. One sample of *V. nitidula* apparently produced only two aglycones (apigenin and luteolin) whereas other samples produced nearly the entire species complement of flavonoids. Some populations of *V. nitidula* exhibited variation in flavonoid profiles between individual plants growing within a few yards of one another. Other populations showed very little or no intrapopulational variation in flavonoids. *Vernonia nitidula* is a wide-ranging species which exhibits morphological variation over its range. Both *V. nitidula* and *V. squamulosa* were previously reported to contain unspecified flavones (Harborne and Williams, 1977).

Table 4. Tentative identity, R_f values, color reactions and major spectral maxima of flavonoids in *Vernonia* subsect. *Chamaedrys*.

		R_f Value[b]		Color[c]		Absorption Maxima in nm[d]					
No.	Identity[a]	TBA	HOAc	UV	UV+ NH_3	MEOH	$AlCl_3$	$AlCl_3$ +HCl	NaOMe	NaOAc	NaOAc +H_3BO_3
A1.	A-7-OMe	.90	.12	P	Y	335 268	352 277	351 277	395 277	373 272	342 265
A2.	Apigenin	.85	.10	P	Y	337 267	350 277	350 277	395 275	379 274	342 268
A3.	Luteolin	.80	.08	P	Y	354 254	426 273	392 274	405 268	383 269	376 264
A4.	L-7-OMe	.80	.10	P	Y	338 258	399 271	352 264	398 268	357 261	362 261
A5.	L-7, 3′-diOMe	.82	.11	P	Y	329 254	332 254	332 254	393 253	325 254	325 253
A6.	L-3′-OMe	.80	.08	P	Y	346 254	410 273	381 267	401 270	365 266	353 268
A7.	Quercetin	.58	.06	Y	Y	372 255	456 270	427 265	DEC	DEC	387 258
A8.	Q-3-OMe	.80	.08	P	Y	353 255	423 273	390 263	405 268	391 270	367 255
1.	Q-7-O diglycoside-3-OMe	.34	.24	P	Y	353 255	429 274	393 272	404 269	374 258	375 258

2.	Q-7-O glycoside-3,3′-diOMe	.48	.21	P	Y	350 251	388 261	388 262	406 258	408 255	351 250
3A.	A-7-O glycoglucoside-3-OMe	.53	.40	P	Y	335 268	382 274	382 274	390 265	342 266	337 267
3B.	A-7-O diglucoside	.53	.40	P	Y	336 267	385 275	385 276	388 268	345 266	338 268
3C.	A-?-glycoside	.53	.40	P	Y	335 270	349 277	348 276	394 279	368 278	343 271
4.	A-6,8-C-diglycoside[e,f]	.23	.80	P	Y	333 272	353 279	352 279	403 283	385 282	324 275
5.	A-6,8-C-diglycoside[g]	.66	.61	P	Y	337 270	356 278	353 278	400 278	383 278	342 271
6.	A-6,8-C-diglycoside-7-0-glycoside[h]	.47	.81	P	Y	271	278	278	272	270	271
6A.	Q-3-O diglycoside	.50	.72	P	Y	360 257	437 275	403 269	416 274	388 271	380 261
6B.	Unknown	.67	.78	P	Y	–	–	-	–	–	–
6C.	A-6,8-C-diglycoside-7-0-glycoside[g]	.29	.85	P	Y	330 268	350 276	349 275	390 275	390 270	328 268
7.	Q-7-O-glucoside-3-OMe	.38	.46	P	Y	353 257	423 273	387 273	407 268	383 259	375 262
8.	Q-7-O glucoside-3,3′-diOMe	.53	.55	P	Y	350 270	388 277	388 275	412 257	375 273	350 272

Table 4. Continued.

No.	Identity[a]	R_f Value[b]		Color[c]		Absorption Maxima in nm[d]					
		TBA	HOAc	UV	UV+ NH_3	MEOH	$AlCl_3$	$AlCl_3$ +HCl	NaOMe	NaOAc	NaOAc +H_3BO_3
9.	Q-7-O-glucoside	.24	.10	Y	Y	362 252	430 256	400 253	DEC	372 252	384 258
10.	Q-7-O glucoside-3'-OMe	.42	.25	Y	Y	358 268	408 264	404 260	DEC	363 268	360 265
11.	A-6,8-C-diglycoside-7-0-glycoside[e]	.18	.38	P	Y	333 268	388 276	387 276	393 269	352 268	340 268
12.	Unknown	.03	.17	P	Y	–	–	–	–	–	–
13.	Flavanone-glycoside	.85	.65	P	DP	294 216	308 217	308 217	329 217	327 218	295 220
14.	Flavanone-glucoside[i]	.81	.41	P	DP	287 214	310 214	310 217	326 217	325 221	287 219
14A.	Unknown	.81	.42	P	DP	---	---	---	---	---	---
15.	Q-3-O-diglucoside-7-O-rhamnoglucoside	.15	.78	P	Y	359 257	428 272	402 268	424 274	382 261	379 260
16.	Unknown	.12	.57	P	P	–	–	–	–	–	–

17.	Unknown	.07	.73	P	P	–	–	–	–	–	–
18.	Unknown	.12	.93	P	P	–	–	–	–	–	–
20.	Unknown	.13	.60	P	Y	–	–	–	–	–	–
20A.	Unknown	.19	.59	P	Y	–	–	–	–	–	–
21.	Unknown	.48	.03	P	Y	–	–	–	–	–	–
22.	Unknown	.00	.13	P	Y	–	–	–	–	–	–
23.	Unknown	.00	.24	P	Y	–	–	–	–	–	–
25.	Q-3,7-O-diglucoside	.35	.38	P	Y	353 255	442 268	400 262	403 266	365 255	370 257
26.	Unknown	.58	.02	P	Y	---	---	---	---	---	---
27.	Unknown	.18	.00	P	P	---	---	---	---	---	---
28.	Flavanone-7-O-glycoside	.78	.61	P	DP	273 215	273 217	273 217	279 217	273 217	273 219

a. A = apigenin, L = luteolin, Q = quercetin. **b.** TBA = tert-butanol:acetic acid: water(3:1:1,v v), HOAc = acetic acid:water (15:85,v v). **c.** P = purple, Y = yellow, D = dark. **d.** First number is Band I peak, second number is Band II peak. **e.** Compound has same sugar at 6 and 8 positions. **f.** Compound has xylose as oxy-sugar attached to 6 and 8 C-sugars. **g.** Compound has different sugars at 6 and 8 positions. **h.** gives compound 5 upon acid hydrolysis; 7-O-sugar not hydrolized by glucosidase **i.** glucose at either 3′ or 4′ position. DEC = decomposed.

Table 5. Flavonoid distribution in *Vernonia* subsect. *Chamaedrys* and hybrids

	Aglycones								O-glycosoides											
	FLA						*FLO*		*FLO*									*FLA*		
Taxon	A1	A2	A3	A4	A5	A6	A7	A8	9	1	7	2	8	10	6A	15	25	3A	3B	3C
Series *Nitidulae:*																				
V. squamulosa		X	X	X	X		X	X	X	X	X						X			
V. nitidula	X	X	X	X	X		X	X	X*	X	X	X	X	X*	X*	X		X		
V. crassa	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X		X	X	X
Series *Chamaedrys:*																				
V. viscidula		X	X				X		X	X				X	X	X		X		
V. laxa		X	X	X			X	X		X		X				X		X		
V. elsieae		X	X	X	X	X	X											X		
V. chamaedrys	X	X	X	X	X	X	X	X	X	X	X	X						X		
V. mucronulata	X	X	X	X	X			X	X	X		X	X				X	X		
V. cuneifolia		X	X	X	X	X			X	X	X	X	X					X		
V. oligactoides		X	X	X	X					X		X	X				X	X		
V. oligolepis	X	X	X	X	X		X	X	X	X	X		X					X	X	
Series *Nudiflorae:*																				
V. chaquensis		X	X	X	X					X	X	X						X		
V. cupularis		X	X	X	X		X	X	X	X		X	X		X	X		X	X	
V. schulziana		X	X	X			X	X	X	X	X							X	X	
V. lucida		X	X	X	X	X	X	X	X	X					X	X		X		
V. nudiflora		X	X	X	X	X	X	X		X	X	X	X		X	X	X	X		
HYBRIDS																				
cr. × nit.		X	X	X					X	X	X	X	X	X	X	X		X	X	
cr. × nud. I		X	X	X	X				X	X	X	X	X		X	X		X	X	
cr. × nud. II		X	X	X	X				X	X	X	X	X		X	X		X	X	
cham. × nud.	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	
oligo. × nud. I	X	X	X	X	X					X	X	X	X			X		X	X	
oligo. × nud. II		X	X	X	X				X	X	X	X			X	X		X	X	
oligo. × oligac.		X	X	X			X			X	X	X	X					X	X	

Table 5. (continued)

Taxon	C-glycosides				Flava.			Unknowns												
	4	5	6	11	6C	14	13	28	12	14A	16	17	18	20	20A	21	22	23	26	27
Series *Nitidulae:*																				
V. squamulosa	X	X	X			X				X	X					X				
V. nitidula	X	X	X			X	X		X	X				X		X				
V. crassa	X	X	X	X		X	X		X	X	X	X	X							
Series *Chamaedrys:*																				
V. viscidula	X	X	X																	
V. laxa		X	X			X	X			X						X			X	
V. elsieae	X	X	X	X			X													
V. chamaedrys	X	X	X	X		X	X		X	X				X		X				
V. mucronulata	X	X	X	X	X	X			X					X						
V. cuneifolia	X	X									X			X		X	X	X		
V. oligactoides	X	X	X			X	X										X	X		
V. oligolepis	X	X	X	X	X	X	X		X					X						X
Series *Nudiflorae:*																				
V. chaquensis	X	X	X			X					X									
V. cupularis	X	X	X			X	X													
V. schulziana	X		X			X														
V. lucida		X	X																	
V. nudiflora	X	X	X																	
HYBRIDS																				
cr. × nit.	X	X	X			X			X					X		X				
cr. × nud. I	X	X	X	X	X	X	X	X						X	X	X				
cr. × nud. II	X	X	X	X		X		X						X	X	X				
cham. × nud.	X	X	X	X		X	X	X						X						
oligo. × nud. I	X	X	X	X										X						
oligo. × nud. II	X	X	X	X		X	X	X						X						
oligo × oligac.	X	X	X	X	X	X		X						X						

Flava. = Flavanone. FLA = Flavone. FLO = Flavonol. * = found in heads only cr. = *V. crassa.* nit. = *V. nitidula.* nud. = *V. nudiflora.* cham. = *V. chamaedrys.* oligo. = *V. oligolepis.* oligac. = *V. oligactoides.*

A similar situation exists with *Vernonia nudiflora* which apparently hybridizes readily with several species. From this species, Mabry et al. (1975) and Abdel-Baset (Ph.D. Dissertation, Univ. of Texas, Austin, 1973) reported several glycosides, including kaempferol-3-O-glycoside and kaempferol-3-O-rhamnoglucoside, which were not found during this study, but they did not find several compounds elucidated here. The samples which they analyzed (including *Timmermann 71127* and *71130*) were collected in northern Argentina (Depto. Cordoba) whereas the samples analyzed for this study came from the state of Paraná, Brazil. An analysis of specimens from throughout the range of this species is thus needed. It may be that *V. nudiflora* is capable of taking on the flavonoid profiles of various species with which it hybridizes in a manner similar to that exhibited by *Dahlia coccinea* Cav. (Giannasi, 1975).

A few samples of tissues other than leaves were examined including phyllaries, achenes, pappus and corollas. In some cases, compounds occurred in the heads which were not found in the leaves of the same species. For example, compounds 6A, 9 and 10 were detected in various head tissues of *Vernonia nitidula* but were not found in its leaves. Head tissues were analyzed in an attempt to show the feasibility of utilizing their flavonoid profiles to help distinguish species and species groups (subseries, series, etc.) in *Vernonia*. Based on these preliminary results, it would seem that flavonoids of head tissues may prove to be very useful and, in the future, should be analyzed in conjunction with the leaf flavonoids whenever feasible.

The flavonoid profiles of those species removed from subsection *Chamaedrys* on morphological grounds were compared to those of species retained in the subsection. The compounds present in the excluded species were not identified; however, all of these species possess two-dimensional paper chromatogram profiles which are obviously different from those of the species retained in subsection *Chamaedrys*.

While the flavonoid data provide little help in delimiting series or subseries within the subsection, they do help in separating the subsection from other subsections of *Vernonia* and clearly point out that the species of subsection *Chamaedrys* are closely related. On the other hand, many of the species in the subsection can be distinguished by differences in their flavonoid profiles. This situation is very similar to the one found in *Arceuthobium* Bieb. (Viscaceae) by Crawford and Hawksworth (1979).

Occurrence of C-glycosides in the subsection is highly significant and sets the group off from other subsections, since these compounds have apparently not previously been found in the genus *Vernonia* (Abdel-Baset, Ph.D. Dissertation, Univ. of Texas, Austin, 1973; Mabry et al., 1975; Harborne and Williams, 1977) although they are known from other genera in the tribe such as *Pollalesta* H. B. K. (Stutts, 1981), *Haplostephium* C. Martius ex DC. and *Lychnophora* C. Martius (Stutts, unpublished; B. L. King, personal communication). The major problem in determining relationships among groups of *Vernonia* is that most species have not been thoroughly analyzed for flavonoids. The results of this survey indicate that once enough taxa have been adequately examined, flavonoids may be highly useful as taxonomic characters at the higher infrageneric levels in *Vernonia* as well as in other larger genera in the tribe Vernonieae.

Palynology

Pollen grains of each species were acetolized by the procedures of Erdtman (1966) and examined utilizing a combination of light microscopy and scanning electron microscopy. Acetolized grains were prepared for scanning electron microscopy by the procedures of Jones (1970).

The external pollen morphology of several species in subsection *Chamaedrys* was examined by Jones (1979a). Jones found these species to have Vernonieae type *A* pollen (subechinolophate, triporate grains with prominent spines) which is considered to be the primitive type for the tribe. Re-examination of these species and examination of all the other species of subsection *Chamaedrys* (sensu Stutts) revealed that all possess type *A* pollen. Several of the species originally assigned to subsection *Chamaedrys* by Jones (1979a) possess type *B* pollen. Those species were removed from the subsection and assigned to other subgeneric groups of *Vernonia*. In summary, the palynological data support the present delimitation of the subsection.

Cytology

Chromosome counts were made from root tips fixed in Carnoy's solution and stained with acetic-orcein. Voucher specimens are deposited at GA (Table 6). The species from which counts were

Table 6. Chromosome counts from *Vernonia* subsect. *Chamaedrys*.

Taxon	Chromosome Number	Voucher*
V. chamaedrys Less.	$2n = 34$	BRAZIL: Paraná, Mun. Ponta Grossa, BR 376, Uvaia, *Stutts 1289;* counts from two plants of this collection.
V. oligolepis Schultz-Bip. ex Baker	$2n = 34$	BRAZIL: Paraná, Mun. Ponta Grossa, BR 376, 1 km W of Vila Velha, *Stutts 1300.*
V. crassa (Vell. Conc.) E. Ekman ex Malme	$2n = 34$	BRAZIL: Paraná, Mun. Balsa Nova, São Louis do Puruna, *Stutts 1008.*
V. nitidula Less.	$2n = 34$	BRAZIL: Minas Gerais, Mun. Passo Quarto, Sertão dos Martius, *Soares Nunes s.n.*
V. nudiflora Less.	$2n = 34$	BRAZIL: Paraná, Mun. Ponta Grossa, BR 376, Rio Tibagi, *Stutts 1180.*
V. chamaedrys Less. × *V. nudiflora* Less.	$2n = 68$	Greenhouse cross of *Stutts 1289* × *Stutts 1180;* counts from two plants of this combination.

*Chromsome counts were made from plants grown from seed of these collections; vouchers deposited at GA.

obtained are *Vernonia chamaedrys, V. oligolepis, V. crassa, V. nitidula* and *V. nudiflora.* All five species were found to be $2n = 34$. Previous counts from the subsection (made from pollen mother cells) include $n = 16$ (Hunter, 1964; Covas and Hunziker, 1954), $n = 32$ (Covas and Hunziker, 1954) and $n = 17$ (Jones, 1974) for *V. nudiflora;* and $n = 17$ for *V. oligolepis* (Jones, 1979b). The chromosome counts presented here support the current hypothesis that *Vernonia* in the New World has a base number of $x = 17$ (Jones, 1979b).

Two counts from different plants of the synthetic hybrid combination *Vernonia chamaedrys* × *V. nudiflora* were $2n = 68$. The chromosome numbers of the actual parent plants of these hybrids are not known so that they may have been either normal diploids ($2n = 34$) or tetraploids ($2n = 68$). Therefore, there are four possible explanations for the polyploid chromosome numbers observed in the hybrids: 1) both parents were tetraploids; 2) the hybrids arose through the fusion of two unreduced gametes; 3) a combination of 1 and 2 where one parent was a tetraploid and the other parent furnished an unreduced gamete; 4) somatic doubling after union of two

normal diploid gametes. Somatic doubling may be the most likely of these four explanations. The previous report of $n = 32$ for *V. nudiflora* (Covas and Hunziker, 1954) suggests that natural polyploids do occur in that species. In fact, several species of *Vernonia* from southern South America have been shown to exhibit polyploid series (Jones, 1974, 1979b).

Hybridization

Hybridization is well known in *Vernonia* (Jones, Faust & Urbatsch, 1970; Miller, 1977; Steyermark, 1939) and some species in subsect. *Chamaedrys* have been reported to hybridize (Malme, 1933). Field observations suggest that some species hybridize in or occupy disturbed sites. In the state of Paranà, Brazil, hybrid swarms involving up to four species of this subsection have been observed. In all, putative hybrids involving ten different parental combinations were observed in the field or as collections by previous workers (Table 7). Specimens intermediate between two good species have created confusion among taxonomists, occasionally leading to the naming of hybrids as species. For example, *V. imbricata* Chodat (Chodat, 1902) appears to be a result of a cross between *V. oligactoides* Less. and *V. oligolepis* Schultz-Bip. ex Baker. The number of hybrids has apparently increased as more habitat disturbance has taken place owing to human activities.

The occurrence of putative natural hybrids within subsection *Chamaedrys* suggested the need to attempt hybridization experiments. All experimental crosses attempted are listed in Table 8. These crosses were made by the technique of Chapman and Jones (1971). Repeated attempts at selfing *Vernonia nudiflora, V. oligolepis, V. chamaedrys* and *V. nitidula* had no success. The first attempts to self *V. crassa* produced several seedlings but additional attempts at selfing this species have failed. Additional attempts to produce hybrids of various combinations of these species (*V. nitidula, V. crassa, V. oligolepis, V. chamaedrys* and *V. nudiflora*) had limited success. In some cases, no viable seed was produced, while in others viable seeds were produced but the germinated seedlings died within a few weeks or months. While many of the cases of seedling death may be attributable to various inviability problems, some may have been due to greenhouse conditions. Only one hybrid combination resulted in the production of mature reproductive plants. The cross *V. chamaedrys* × *V. nudiflora* resulted in the production of

Table 7. Putative hybrids of *Vernonia* subsection *Chamaedrys*

Hybrid combinations	Specimens
V. chamaedrys × *V. mucronulata:*	*P. Dusen 9823* (S): BRAZIL, Paraná, Porto Amazonas, in campo, April 26, 1910.
V. chamaedrys × *V. nudiflora:*	*Hassler 9136* (BM, G, NY): PARAGUAY, near Caaguazú, 1905. Hassler 9189 (BM): Paraguay, near Caaguazú, 1905. *Stutts 1291* (GA): BRAZIL, Paraná, Mun. Ponta Grossa, campo, March 5, 1982.
V. chamaedrys × *V. oligactoides:*	*Stutts 1292* (GA): BRAZIL, Paraná, Mun. Ponta Grossa, campo, March 5, 1982.
V. chamaedrys × *V. oligolepis:*	*P. Dusen 3942* (S): BRAZIL, Paraná, Capão Grande, Ponta Grossa, in campo, March 1, 1904. *P. Dusen 4219* (S): BRAZIL, Paraná, Capao Grande, Ponta Grossa, in campo, March 20, 1904. *E. Pereira 5241* (F): BRAZIL, Paraná, Ponta Grossa, Vila Velha, February 10, 1960.
V. crassa × *V. nitidula:*	*Stutts 1010* (GA): BRAZIL, Paraná, Mun. Balsa Nova, borda da Cuesta Devoniana, October 25, 1980.
V: crassa × *V. nudiflora:*	*P. Dusen 14831* (G, GH, NY, S): BRAZIL, Paraná, Vila Velha, campo rupestri, April 29, 1914. *P. Dusen & Jonsson 200a* (S): BRAZIL, Paraná, Vila Velha, campo rupestri, April 27, 1914.
V. mucronulata × *V. oligactoides:*	*P. Dusen 11730* (S): BRAZIL, Paraná, Mun. Jaguariaiva, May 2, 1911. *P. Dusen s.n.* (S): BRAZIL, Paraná, Mun. Jaguariaiva, April 11, 1910. *P. Dusen s.n.* (S): BRAZIL, Paraná, Guarapuava, in campo, January 11, 1911. *P. Dusen 16708* (GH, S): BRAZIL, Paraná, Mun. Jaguariaiva, Feburary 18, 1915. *P. Dusen 16930* (S): BRAZIL, Paraná, Capão Bonito, campo, March 30, 1915. *Stutts 1293* (GA): BRAZIL, Paraná, Mun. Ponta Grossa, BR 376 ca. 22 km W of Ponta Grossa, grazed campo, March 5, 1982.
V. nudiflora × *V. oligolepis:*	*R. Reiss 43A* (NY): BRAZIL, Paraná, March 2, 1935. *Stutts 1280* (GA): BRAZIL, Paraná, Mun. Palmeira, Colonia Francesca, BR 277, 3 km E of Rio Capivara, campo, March 4, 1982. *Stutts 1288* (GA): BRAZIL, Paraná, Mun. Ipiranga, BR 373, 23 km E of Imbituva,

Table 7. Continued.

Hybrid combinations	Specimens
	grazed campo, March 5, 1982. *Stutts 1301* (GA): BRAZIL, Paraná, Mun. Ponta Grossa, Vila Velha, BR 376, disturbed campo rupestri, March 6, 1982. *Stutts 1305* (GA): BRAZIL, Paraná, Mun. Ponta Grossa, BR 376, Rio Barrozinha,
V. oligactoides × *V. oligolepis:*	*Hassler 1861* (G): PARAGUAY, near Peribebury, ad marginem silvae, February, *Balansa 963* (G): PARAGUAY, dans les paturages. *Stutts 1204* (GA): BRAZIL, Paraná, Mun. Jaguariaiva, Estrada do Arapoti, heavily grazed campo, February 16, 1982. *Stutts 1216* (GA): BRAZIL, São Paulo, Mun. Itararé, Fazenda Esplanada, campo-cerrado intermediate, February 17, 1982.

numerous offspring, six of which produced flowers. These plants exhibit a range of morphological variation with some individuals closer to *V. chamaedrys* and others closer to *V. nudiflora* in their gross morphology, while still others are intermediate in character. Voucher specimens of these plants are deposited at GA (Table 8).

Pollen viability of both the parents and the synthetic hybrids was checked by staining pollen grains with aceto-carmine in glycerine jelly as described by Radford, et al. (1974). The hybrids exhibited pollen viability essentially equal to or only slightly lower than that of the parents (Table 9).

Conclusions from Biosystematic Studies

The extreme similarity of sesquiterpene lactone profiles for species tested is an indication that these species are closely related. The presence of C-glycoflavones in all species of the subsection separates this group from other groups of *Vernonia* whose flavonoid profiles have been examined, all of which apparently lack C-glycosides. While no absolute differences in flavonoids were found at either the series or subseries level, many species have distinct flavonoid profiles. The relative uniformity of the flavonoid chemistry of the subsection suggests a close relationship among the species. Knowledge of the flavonoid chemistry of the subsection will be useful for comparison with other major groups within *Vernonia* once these taxa

Table 8. Attempted hybridizations in *Vernonia* subsect. *Chamaedrys*.

Combination	Viable Seed Produced	Reproductive Individuals Produced	Voucher*
V. crassa (Vell. Conc.) E. Ekman ex Malme SELFED	+	–	BRAZIL: Paraná, Mun. Balsa Nova, São Louis do Puruna, *Stutts 1008*.
V. nitidula Less. SELFED	–	–	BRAZIL: Minas Gerais, Mun. Passo Quarto, Sertão dos Martius, *Soares Nunes s.n.*
V. chamaedrys Less. SELFED	–	–	BRAZIL: Paraná, Mun. Ponta Grossa, BR 376, Uvaia, *Stutts 1289*.
V. oligolepis Schultz-Bip. ex Baker SELFED	–	–	BRAZIL: Paraná, Mun. Ponta Grossa, BR 376, 1 km W of Vila Velha, *Stutts 1300*.
V. nudiflora Less. SELFED	–	–	BRAZIL: Paraná, Mun. Ponta Grossa, BR 376, Rio Tibagi, *Stutts 1180*.
V. crassa × *V. nitidula*	+	–	*Stutts 1008* × *Soares Nunes s.n.*
V. chamaedrys × *V. oligolepis*	+	–	*Stutts 1289* × *Stutts 1300*
V. chamaedrys × *V. nudiflora*	+	–	*Stutts 1289* × *Stutts 1180*

*Plants used in attempted hybridizations were grown from seed of these collections; vouchers deposited at GA.

are surveyed. Overall flavonoid chemistry strongly supports the taxonomic treatment presented here.

The fact that all species of the subsection have type *A* pollen further indicates relationship among these species. Chromosome counts obtained from various species and one artificial hybrid combination fit previously observed patterns in the genus. Several species of the subsection can be induced to hybridize while many others apparently form natural hybrids, as shown by production of viable seed. This behavior indicates a high degree of interrelatedness among these species.

Table 9. Pollen viability of *Vernonia chamaedrys, V. nudiflora* and their hybrids.

Taxon	% Viable Pollen	Voucher*
V. chamaedrys Less.	95%	BRAZIL: Paraná, Mun. Ponta Grossa, Br 376, Uvaia, *Stutts 1289.**
V. nudiflora Less.	92%	BRAZIL: Paraná, Mun. Ponta Grossa, Br 376, Rio Tibagi, *Stutts 1180.**
V. chamaedrys Less. × *V. nudiflora* Less.		Greenhouse cross of *Stutts 1289* × *Stutts 1180.*
plant 1	92%	
plant 2	94%	
plant 3	87%	
plant 5	88%	
plant 9	94%	
plant 13	87%	

*Parental species grown from seed of these collections; vouchers deposited at GA.

PART III:
TAXONOMIC TREATMENT

Vernonia subsect. **Chamaedrys** Cabrera, Darwiniana 6: 307. 1944.

TYPE SPECIES: *Vernonia chamaedrys* Less.

Fruticose or suffrutescent perennials with a xylopodium or shrubs without a xylopodium. Leaves alternate, petiolate or sessile; blades linear, lanceolate, elliptic, ovate or oblanceolate, acuminate to obcordate at the apex, attenuate to cordate at the base, glabrous to tomentose above, glabrous to tomentose to lanuginose below, thinly to densely punctate-glandular above and below, margins entire to serrate to crenate. Inflorescences corymbose-paniculate or thyrsoid-paniculate. Heads small to medium-sized, generally numerous, sessile to pedicellate, with 4 30 florets. Involucres turbinate to campanulate; phyllaries imbricate in several series. Corollas purple to white. Pappus biseriate; inner bristles numerous. Achenes pubescent to glabrous, thinly to densely glandular-dotted.

KEY TO THE SERIES, SUBSERIES AND SPECIES
OF SUBSECT. *CHAMAEDRYS*

A. Shrubs without a xylopodium, generally having several highly branched stems ..... Series *Nitidulae*. B.
B. Leaves lanate below; heads with 20–30 florets; achenes 3–4 mm long ..... 1. *V. crassa*.
B. Leaves glabrous to tomentose below; heads with 5–15(17) florets; achenes 2–3 mm long ..... C.
C. Corollas 6.5–9(10) mm long, the tube ca. 1.5 times as long as the lobes; involucres (4.5)5–8(12) mm in height, of 25–35 bracts arranged in 6–8 series; (5)6–11(13) florets per head; leaves sessile to subsessile, becoming glabrous below with age, typically narrowly oblanceolate but varying from almost linear to ovate to lanceolate. [Geographic Distribution: Northeastern Argentina from the Rio de La Plata north to Paraguay and across to southern Minas Gerais, Brazil.] ..... 2. *V. nitidula*.
C. Corollas (8.5)9–12(13) mm long, tube ca. 2 times as long as the lobes; involucres 9–14 mm in height, of 40–50 bracts arranged in 7–9 series; (10)11–15(17) florets per head; leaves subsessile to obviously petiolate, the petioles 0.1–0.6 cm long, puberulent to tomentose below (rarely essentially glabrous), typically elliptic but varying from narrowly elliptic to lanceolate or rarely oblanceolate. [Geographic Distribution: Southern Bolivia and northwestern Argentina in the foothills of the Andes.] ..... 3. *V. squamulosa*.
A. Fruticose or suffrutescent perennials with a xylopodium, having one to several stems from the xylopodium, generally not highly branched except in the inflorescence ..... D.
D. Inflorescence thyrsoid-paniculate; heads sessile or very short-pedicellate (pedicels 0.1–3(5) mm long) and arranged in glomerules or small compact cymose groups at the ends of the peduncles; involucres turbinate to approaching campanulate ..... Series *Chamaedrys*. E.
E. Stems viscid-pubescent, or leaves strigose-pubescent above (sometimes becoming nearly glabrous with age) or scabrous above. [Inflorescence laxly thyrsoid-paniculate.] ..... Subseries *Laxae*. F.
F. Stems viscid-pubescent; inner involucral bracts acuminate at the apex ..... 4. *V. viscidula*.

F. Stems not viscid-pubescent; inner involucral bracts rounded to acute at the apex ..... G.

G. Leaves, sessile, linear, 10–15 times as long as wide, margins entire .....5. *V. elsieae.*

G. Leaves subsessile (petioles 1–3 mm long), elliptic to oblanceolate, 2–3 times as long as wide, margins serrate to serrulate .....6. *V. laxa.*

E. Stems glabrous to tomentose (not viscid-pubescent) and leaves essentially glabrous above (not strigose-pubescent or scabrous). [Inflorescence densely thyrsoid-paniculate.] ..... Subseries *Chamaedrys.* H.

H. Stem leaves linear to linear-lanceolate, (3)4–7(9) mm wide; leaf margins entire or very rarely having a few minute and obscure teeth; heads with (4)5(6) florets; inner pappus of ca. 75–100 bristles ..... 11. *V. oligolepis.*

H. Stem leaves oblanceolate, ovate or elliptic, 15–50(60) mm wide; leaf margins serrate to serrulate or crenate, rarely entire; heads with (5)6–25 florets; inner pappus of ca. 35–65 bristles ..... I.

I. Involucral bracts of mature heads lanose on dorsal surface; heads with (15)20–25 florets ..... 10. *V. oligactoides.*

I. Involucral bracts of mature heads glabrous on dorsal surface or ciliate along margins or the outer (lower) bracts somewhat puberulent but never lanose; heads with (5)6–13(16) florets ..... J.

J. Heads sessile; mature achenes 3–4 mm long; leaves white to grayish tomentose below; leaf margins serrate to serrulate or denate ..... 7. *V. chamaedrys.*

J. Heads mostly subsessile to short pedicellate; (pedicels 1–3 mm long; some heads may be sessile); mature achenes 2–2.5(2.8) mm long; leaves typically brownish tomentose below, sometimes grayish; leaf margins crenate-serrate, serrulate or entire.. ..... K.

K. Leaves elliptic, occasionally ovate to oblanceolate; upper leaves and bracts of inflorescence cordate to rounded at base, lower leaves varying from cuneate to cordate at the base; leaf apices

mucronate; leaf margins crenate-serrulate or entire; heads with (5)6–10(11) florets; inner phyllaries acute at the apex; achenes thinly pubescent and glandular-dotted . . . . . 8. *V. mucronulata.*

K. Leaves obovate; all leaves and bracts of inflorescence cuneate at base; leaf apices obtuse to rounded; leaf margins serrulate to serrate, occasionally crenate-serrulate, near apex; heads with (7)10–12(15) florets; inner phyllaries rounded to obtuse at the apex; achenes glabrous to thinly pubescent, densely glandular-dotted. [Plants from western portions of the species range tend to have thinly pubescent achenes.] . . . . . 9. *V. cuneifolia.*

D. Inflorescence corymbose-paniculate; most heads obviously pedicellate (pedicels (1)4–8(35) mm long) and arranged in corymbs at the ends of the peduncles; involucres campanulate to approaching turbinate . . . . . Series *Nudiflorae.* L.

L. Leaves linear (1–2 mm wide) and inner pappus 5–7 mm long and involucral bracts in 4–5 series or leaves linear lanceolate (4–15 mm wide) and having (7)8–13 florets per head and inner pappus 5–6 mm long and involucral bracts in 3–4 series . . . . . Subseries *Nudiflorae.* M.

M. Leaves linear, 1–2 mm wide, the margins strongly revolute, the lower surface sericeous (often obscured by revolute margins) . . . . . 12. *V. nudiflora.*

M. Leaves linear-lanceolate, 4–15 mm wide, the margins serrulate and subrevolute, the lower surface with very short scabrous hairs . . . . . 13. *V. lucida.*

L. Leaves not as above or leaves linear (3–10 mm wide) and inner pappus 8–9 mm long and involucral bracts in 6 or more series or leaves narrowly lanceolate, narrowly elliptic or oblanceolate (10–25 mm wide) and having (12)15–20 florets per head and inner pappus 5.5–7 mm long and involucral bracts in 4–6 series . . . . . Subseries *Chaquenses.* N.

N. Involucres 12–15 mm in height; inner pappus 8–9 mm long; involucral bracts in 6 or more series . . . . . 14. *V. cupularis.*

N. Involucres 6–8 mm in height; inner pappus 5.5–7 mm long; involucral bracts in 4–6 series . . . . . O.

O. Heads with (12)15–16 florets; involucral bracts tomentose at the apex; leaves narrowly elliptic to oblanceolate, cuneate to attenuate at the base, not scabrous above ..... 15. *V. chaquensis.*

O. Heads with 18–20 florets; involucral bracts glabrous at the apex; leaves narrowly lanceolate, rounded at the base, scabrous above ..... 16. *V. schulziana.*

Vernonia series **Nitidulae** (Cabrera) Stutts, *stat. nov.*

Vernonia subsect. *Nitidulae* Cabrera, Darwiniana 6: 347. 1944. TYPE SPECIES: *Vernonia nitidula* Less.

Shrubs without a xylopodium, generally having several highly branched stems; leaves varying from linear to elliptic to ovate to oblanceolate; inflorescences corymbose-paniculate; heads numerous, with 5–30 florets.

1. *Vernonia crassa* (Vell. Conc.) E. Ekman ex Malme, Kongl. Svenska Vetenskapsakad. Handl. Ser. III, 12(2): 24. 1933. [As *Vernonia crassa* E. Ekman with no reference to a type. Lists *P. Dusen 8059, 14807, 209a,* and *973a* as a representative which have previously been considered to be syntypes but does not mention basionym.]

Chrysocoma crassa Vell. Conc., Florae fluminensis: 305. 1825. TYPE: not designated. [Gives reference to diagram Vol. 8, table 8 which is clearly this species but was not published until 1835, not 1827 as listed. A search for Vellozo's original specimens deposited at 'Cabinet d'Histoire Naturelle de Rio de Janeiro' revealed that they are no longer at that location and are thought to have been destroyed.] NEOTYPE here designated: BRAZIL. Paraná: Vila Velha, in campo rupestri, 875 m, April 28, 1914, *P. Dusen & Jonsson 209a* (GH!; ISONEOTYPES: A!, G!, S!).

Highly branched shrub up to 1.5 m tall; stems densely tomentose. Leaves cauline, subsessile to short petiolate; petioles 0.1–0.6 cm long, densely tomentose; blades ovate to narrowly elliptic, 3–6 cm long, (0.5)1.5–2.5 cm wide, length/width ratio 2–3.5(5), lustrous and densely punctate-glandular above at maturity, densely greyish to brownish tomentose beneath; obtuse to acute at the apex; cuneate at the base; margins remotely serrate (especially near apex) to entire. Inflorescences corymbose-paniculate. Heads with 20–30 florets, subsessile or short pedicellate; pedicels up to 10 mm long. Involucre urceolate-campanulate, (0.9)1.2–1.7(2.2) cm tall; phyllaries imbricate in 8–10 series, often with reduced bracts extending down the pedicel; inner phyllaries ciliate along the margins, less so with age,

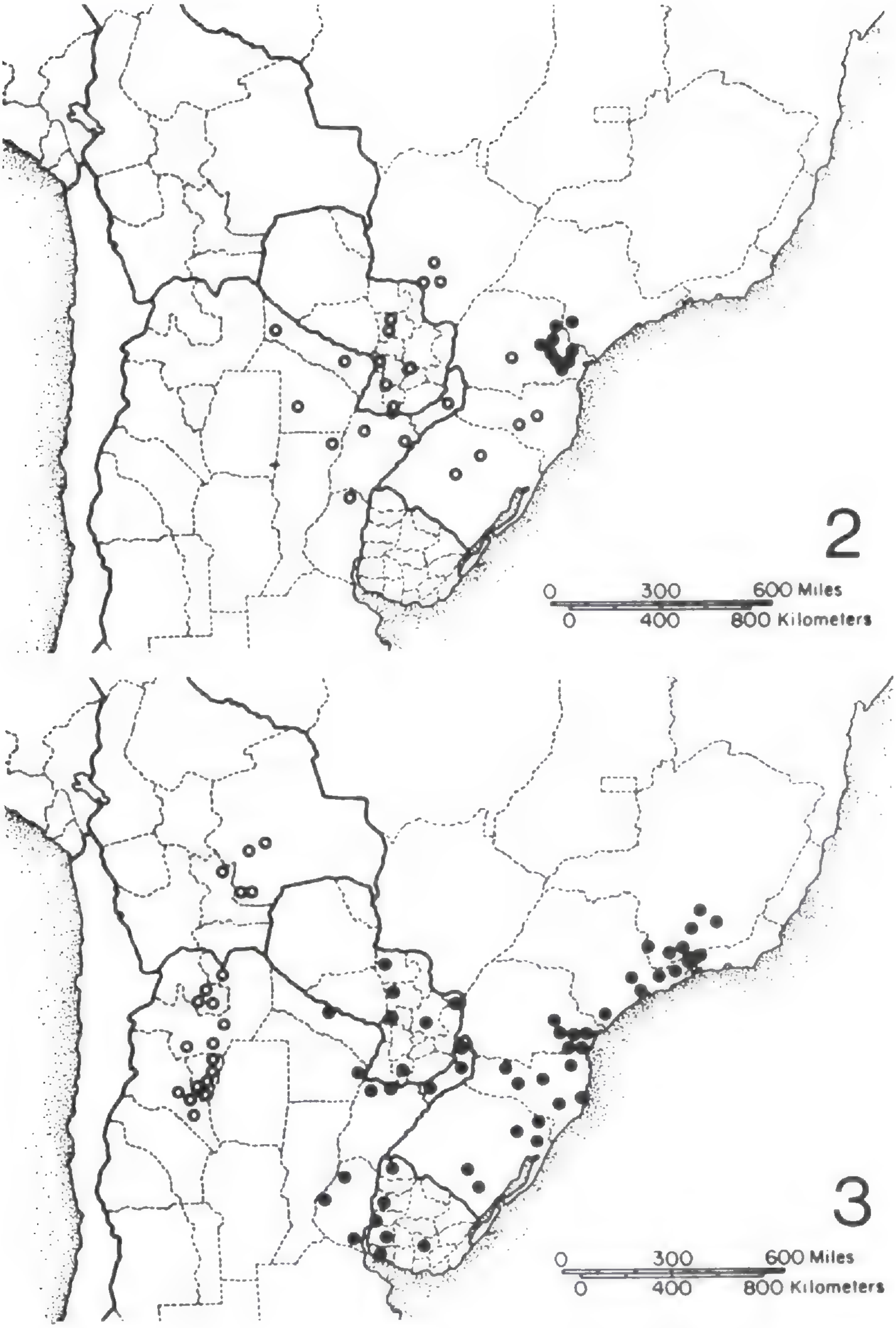
often purple at the tip, (5.5)6–7.5 mm long, 1.3 -2.5 mm wide, obtuse to rounded at the apex; outer phyllaries ciliate at margins, 1.4 2(2.9) mm long, 0.6–1.2(1.4) mm wide, acute at the apex. Corollas rosy-purple, lightly scented, the tube 5.5 6.5(7.2) mm long, the lobes 3.5 4(4.5) mm long, the tube (1.5)1.7(2.1) times as long as the lobes. Anthers 3.5 4 mm long. Style branches 2.5 -3.5 mm long. Pappus straw-colored; inner series of ca. 40 -55 bristles (5.5)6–7(7.5) mm long; outer series 0.5 1.5 mm long. Achenes thinly pubescent and glandular-dotted, 3 4 mm long, 0.7 1.1 mm wide, length/ width ratio ca. 3–4.

Vernonia crassa occurs in the state of Parana and one small area in the state of São Paulo, Brazil (Figure 2). This species is found in scattered localities, often forming low dense patches among the rocks and surrounding campo of sandstone outcrops on and along the margins of the second planalto at elevations of ca. 800–1200 m. Flowering takes place mostly in September and October but some individuals flower from July to February.

Vernonia crassa is easily distinguished from other species in this series by its lanate lower leaf surfaces and the larger number of flowers per head. The attractive flowers and foliage give the species some potential as an ornamental.

Despite its distinctive appearance some confusion exists regarding *V. crassa*. The name *V. rigiophylla* Schultz-Bip. ex Baker (= *V. elsieae* Stutts) is often misapplied to specimens of *V. crassa* which have unusually narrow leaves. This condition is often seen in plants growing in crevices of rocks and at higher altitudes.

It seems preferable to designate a neotype rather than designating the diagram in the 1835 publication as a lectotype since this publication is rare and morphological details are obscure. *P. Dusen and Jonsson 209a* was chosen as the neotype for a variety of reasons. This collection was listed by Malme (1933) when he published Ekman's transfer of the species into *Vernonia* and thus would be preferable to selecting a more recent collection not seen by previous workers. The other collections listed by Malme (1933) are less desirable for use in typification since some, but not all, sheets of both *P. Dusen 8059 and 973a* appear to be hybrid derivatives and I have seen only one sheet of *P. Dusen 14807* (S). On the other hand there are at least five sheets of *P. Dusen and Jonsson 209a* extant and all seem to be good *V. crassa* (i.e., not hybrid derivatives). Some of the specimens of these Dusen collections also bear the name Jonsson whereas other sheets of the same number do not. However, this does



Figures 2 and 3. Distribution of *Vernonia* subsect. *Chamaedrys* in southern South America. **2.** *V. crassa* (●) and *V. chamaedrys* (o). **3.** *V. nitidula* (●) and *V. squamulosa* (o).

not present any real problem since Dusen's name always appears on the labels.

REPRESENTATIVE SPECIMENS: **Brazil:** SÃO PAULO: Itarare, campo limpo, August 28, 1969, *H. F. L. Filho 867* (NY, RB). PARANÁ: Mun. Senges, Morro Pelado, July 16, 1971, *Hatschbach 26761* (MBM, S); Mun. Pirai do Sul, Joaquim Murtinho, 3–5 km S of Rio Lambari, campo rupestri, 1000 m alt., February 15, 1982, *Stutts 1192* (GA, MBM); Mun Tibagi, Pedra Branca, junto a Cuesta Devoniana, September 7, 1966, *Hatschbach 14693* (MBM, US); Mun. Ponta Grossa, Vila Velha, February 4, 1909, *P. Dusen 7728* (A, M, S); Mun. Palmeira, Col. Wietmarsum, campo, afloramentos de arenito, September 27, 1968, *Hatschbach 19881* (MBM, UC); Mun. Balsa Nova, Alto Puruna, just W of Sao Louis do Puruna, edge of second planalto, alt. ca. 1160 m, October 25, 1980, *Stutts 1008* (GA, MBM); Mun. Curitba, Serra do Puruna, estrada Palmeira-Curitiba, campo limpo, *G. Tessmann 2472* (RB); Mun. Bocaiuva do Sul, Santa Ana, October 4, 1971, *Hatschbach 27086* (MBM, S, UC).

2. *Vernonia nitidula* Less., Linnaea iv: 266. 1829. TYPE: BRAZIL. Legit ad Rio das Pedras alissque locis in Campis, Octbr. annis 1826–28, *Sellow s.n.* (HOLOTYPE: not extant); LECTOTYPE here designated: (Isotype at G-DC, as IDC microfiche!).

Baccharis montevidensis Sprengel, Systema Vegetabilium III: 460. 1826. TYPE: Monte Video, *Sellow s.n.* (HOLOTYPE: P; ISOTYPES: BR(2)!, MO!).

Vernonia gochnatioides Hook. et Arn. ex DC., Prodromus 7: 264. 1838. TYPE: not designated. NEOTYPE here designated: URUGUAY: Depto. Colonia, Rio San Juan, November 13, 1936, *Cabrera 3882* (NY! ISONEOTYPE: S!).

Vernonia florida Gardner, Hook. Lond. Journ. Bot. 5: 212. 1846. TYPE: BRAZIL: Minas Gerais, campos near Cattas Altas, September 1840, *Gardner 4803* (HOLOTYPE: BM!; ISOTYPES: F(fragment), G!, GH!, NY!, S!, W—as photo F!).

Vernonia nitidula Less. var. *florida* (Gardner) Baker, Mart. Fl. Brasil 6: 115. 1873.

Vernonia nitidula Less. var. *acutifolia* Griseb., Symbolae ad floram argentinam: 166. 1879. TYPE: not designated. [No authentic examples seen.]

Cacalia gochnatioides (Hook. et Arn. ex DC.) Kuntze, Rev. Gen. Plant. 2: 970. 1891.

Cacalia montevidensis (Sprengel) Kuntze, Rev. Gen. Plant. 2: 968. 1891.

Vernonia arechavaletae Andre, Rev. Hort. 73: 284. 1901. TYPE: LECTOTYPE selected from among syntypes: URUGUAY: Entre arbustos dela Sierra de Minas, *Arechavaleta 25* (K!).

Vernonia nitidula Less. var. *intermedia* Chodat, Bull. Herb. Boissier Ser. II, 1: 408. 1901. TYPE: LECTOTYPE selected from among syntypes: PARAGUAY: in palude pr. San Bernardino, *Hassler 884* (G-DEL!).

Highly branched shrub up to 3 m tall; stems ascending, essentially glabrous or pubescent. Leaves cauline, somewhat reduced upwards, sessile to subsessile, generally somewhat ascending; blades typically narrowly oblanceolate, (2)3–6(9) cm long, (0.3)0.5–1(3) cm wide, length/width ratio (1.5)5–8(14); lustrous and punctate-glandular above, becoming glabrous with age above and below; acute to

obtuse at the apex; cuneate to attenuate, rarely rounded at the base; margins entire to serrate, often serrulate near the apex. Inflorescences corymbose-paniculate. Heads with (5)6–11(13) florets; pedicels 1–12 mm long. Involucres turbinate, (4.5)5–8(12) mm tall; phyllaries 25–35, imbricate in 6–8 series, often with reduced bracts extending down the pedicel; inner phyllaries glabrous, usually thinly glandular near the apex, often purple at the tip, (2.7)3.2–5(6.5) mm long, 0.8–2 mm wide, obtuse to acute at the apex; outer phyllaries glabrous, (0.3)0.5–0.8(1.1) mm long, 0.3–0.7 mm wide, obtuse to acute at the apex. Corollas purple, often fading to white, the tube (4)4.5–6(6.5) mm long, the lobes (2.5)2.7–3.8(4.2) mm long, the tube (1.3)1.5(1.8) times as long as the lobes. Anthers 3–4 mm long. Style branches (2)2.3–3(4) mm long. Pappus typically straw-colored, occasionally purple; inner series of 40–60 bristles (4.5)5–6(6.5) mm long; outer series 0.4–1 mm long. Achenes pubescent and glandular-dotted, 2–3 mm long, (0.5)0.7–1 mm wide, length/width ratio ca. 2–3.

Vernonia nitidula is the widest ranging species of subsect. *Chamaedrys,* occurring from the Rio de La Plata in northern Argentina north to Paraguay and across to southern Minas Geraís, Brazil (Figure 3). Flowering occurs from late August through early December, peaking in October.

Vernonia nitidula prefers full sun or partial shade and seems to be adapted to a wide variety of soil and moisture conditions. In Brazil, it is very common in the Atlantic Forest zone in open or disturbed sites along the margins of forests and campos, along roadsides where it often forms dense stands. There is the possibility that the species may be excluded from the campos by fire. *Vernonia nitidula* also occasionally is found in areas of secondary vegetation on slopes or other slightly raised sites in the Fluvial Coastal Forest zone of Brazil. In Argentina, Uruguay and Paraguay, this species is more often found on moist or wet sites.

The large amount of phenotypic plasticity exhibited by *V. nitidula* has confused taxonomists unfamiliar with the species throughout its range. The species has been treated as several discrete taxa which are not recognized here because of the lack of morphological discontinuities. One taxon not worthy of specific recognition but often treated as a species by modern workers, *V. florida* Gardner, differs from the norm by having larger and more lanceolate leaves. However, the modern descriptions of this taxon do not agree with the actual characters of its holotype which is fairly typical of *V.*

nitidula from Minas Gerais, Brazil. Intensive studies are needed to determine whether any infraspecific taxa within this species are worthy of recognition. Until such documentation is available, it is better to avoid naming of morphological variants.

Vernonia nitidula is most easily confused with *V. squamulosa* Hook. & Arn. but since the two species are allopatric their similar appearance should create little difficulty for the field botanist. *Vernonia nitidula* is more highly branched and densely leaved than *V. squamulosa,* has generally smaller leaves, heads and floral parts and the leaves are typically smooth above, whereas those of *V. squamulosa* are typically slightly scabrous.

REPRESENTATIVE SPECIMENS: **Brazil:** MINAS GERAIS: São João del Rio, October, 1896, *A. Silveira 1670* (RB); BR 40, ca. 13 km N of Santos Dumont, 720 km S of Brasilia, October 2, 1980, *Stutts 857* (GA, RB); Mun. Andrelandia, Cruz das Almas, sujo, August 23, 1936, *Mello-Barreto 5211* (SP); Caldas, *A. F. Regnell 206* (NY, S, US); Sapucaí, Mirim, Serraria Boa Vista, October 26, 1950, *M. Kuhlmann 2593* (RB, SP); Mun. Passo Quarto, Distrito do Pinheirinhos, Sertão dos Martins, October 6, 1979, *Soares Nunes 174* (RB). RIO DE JANEIRO: Serra do Itatiaia, October 22, 1903, *P. Dusen 2188* (S); Serra do Itatiaia, October 23, 1928, *Porto 1794* (RB). SÃO PAULO: Serra do Bocaina, Bananal, October, 1949, *A. C. Brade 20127* (LP, RB, S); Campos do Jordão, *Hashimoto 6* (RB); Mun. Sta. Isabel, Igarata, September 28, 1950, *M. Kuhlmann 2568* (RB, SP); Jundiaí, October 18, 1953, *Hoehne 3908* (RB); Estacão Pilar, between São Paulo and Santos, September 28, 1898, *Edwall 4287* (SP); Eldorado, October, 1940, *Ivan Hauff 52* (SP). PARANÁ: Mun. Ponta Grossa, October 16, 1910, *P. Dusen 10308* (BM, GH, MO, S); Mun. Palmeira, 4 km W of Palmeira, October 14, 1966, *J. L. Lindeman & J. H. Haas 2701* (US); Mun. Campo Largo, October, 1964, *M. L. Pereira 9* (RB); Mun. Curitiba, Taruma, October 18, 1971, *Hatschbach 27657* (MBM, S); Mun. S. Jose dos Pinhaes, Quarto Pinheiros, September 19, 1960, *Hatschbach 7252* (MBM, RB); Mun. Morretes, Serra Marumbi, Pico Olimpo, Lage do Almoco, October 11, 1947, *Hatschbach 774* (MBM, RB); Mun. Lapa, in paludosis, October 9, 1908, *P. Dusen 6839* (S); Mun. Tijucas do Sul, near Tabatinga, ca. 0.2 km W of BR 376, October 23, 1980, *Stutts 1005* (GA, MBM); Itaperussu, in campos ad marg. silva, November 18, 1908, *P. Dusen 7154* (GH, MO, NY, S, UC); Pinhaes, in paludosis, October 1, 1910, *P. Dusen 10329* (A, GH, M, MO, S). SANTA CATARINA: Abelardo Luz, campo, October 23, 1964, *L. B. Smith 12888* (LP, RB, US); Catanduvas, October 12, 1964, *L. B. Smith 12446* (LP, RB, US); Lebon Regis, Rio dos Patos, orla de pinhal, October 29, 1962, *P. Reitz & R. M. Klein 13869* (LP, RB); Campo Alegre, 4 km S C. Alegre on road to Jaraguá do Sul, campo and pinheiral, November 6, 1956, *L. B. Smith & R. M. Klein 7331* (LB, RB, US); Bom Retiro, campo between Fazenda Campo dos Padres and F. Santo Antonio, November 21, 1956, *L. B. Smith 7792* (LB, RB, US); Piloes, Palhoca, along river, September 28, 1956, *P. Reitz & R. M. Klein 3783* (LP, NY, RB, S, US). RIO GRANDE DO SUL: Bom Jesus, Rio Pelotas, October 23, 1961, *E. Pereira 6417* (RB); Farroupilha, in dumetosis, October 4, 1957, *(O. Camargo 62031* (S); Taimbesinho, S. Frsco. de Paula, November 11, 1951, *B. Rambo 51368* (S); Cacapava do Sul, cuminho da Cruta do Segredo, October 31, 1961, *E. Pereira 6611* (LP, RB); Piratini, in ora silvado, November 3, 1901, *Malme 193* (S). **Paraguay:** Itiati, common in meadows, November 5, 1928, *P. Jorgensen 4430*

(GH, MO, NY, RB, S). DEPTO. CONCEPCION: Concepcion, margin silvas, juxta flum. Paraguay, in campo graminoso, September 17, 1893, *Malme 952* (BM, GH, S); DEPTO. MISIONES: Santiago, Estancia La Soledad, September 24, 1962, *T. M. Pedersen 6542* (GH, US); DEPTO. CAAGUAZÚ: Caaguazú, September, 1905, *Hassler 9418* (BM, GH, NY, UC); DEPTO. LA CORDILLARA, 1913, *Hassler 11827* (BM, GH, MO, NY, UC); DEPTO. SAN PEDRO: Alto Paraguay, Primavera, swampy campo, September 9, 1954, *A. L. Woolston 317* (NY, S); DEPTO. ALTO PARANÁ, matorral, October 14, 1952, *Montes 12711* (M). **Argentina:** FORMOSA: Depto. Pilcomayo, Ruta 86, km 68-69, October 30, 1948, *T. Morel 6438* (NY); CHACO: La Palmas, campo, *P. Jorgensen 2035* (MO); CORRIENTES: Depto. Empedrado, Estancia La Yela, September 24, 1959, *T. M. Pedersen 5092* (BR, G, S, UC); MISIONES: Iguazú, Puerto Istueta, September 27, 1950, *Montes 9348* (NY); ENTRE RIOS: Rio Ceibo, delta del Paraná, November 23, 1931, *Cabrera 1937* (NY, UC). **Uruguay:** DEPTO, ARTIGAS, Catalan, November 27, 1928, *G. Herter 485 B* (GH, M, MO, NY, UC); DEPTO. PAYSANDÚ, Arroyo Negro, November 12, 1937, *Rosengurtt B-2250* (GH, NY); DEPTO. DE RIO NEGRO: Orillas del Rio Uruguay, Rincón del las Gallinas, arroyo de los Patos, Estancia de Goenaga, October 22–23, 1942, *Rosengurtt B-4071* (LP, MO, SP); DEPTO. SORIANO: Juan Jackson, Estancia Sta. Elena, December, 1935, *Rosengurtt et al. B-158* (MO, SP); DEPTO. FLORIDA, Estancia Rincon de Santa Elena, Picada Castro, arroyo Mansa Villagra, December, 1946, *Rosengurtt B-5828* (BR, MO, S); DEPTO. COLONIA: Riachuelo, November 15, 1936, *Cabrera 3910* (LP).

3. *Vernonia squamulosa* Hook. et. Arn., Companion Bot. Mag. 2: 44. 1836. TYPE: ARGENTINA: Plentiful in the woods of Tucuman, *Tweedie 1224* (HOLOTYPE: K!).

Cacalia squamulosa (Hook. et Arn.) Kuntze, Rev. Gen. Plant. 2: 971. 1891.

Cacalia praecox Kuntze, Rev. Gen. Plant. 3: 139. 1898. TYPE: ARGENTINA: Jujuy [No collector or collection number given. Kuntze's herbarium and extant types are now at NY.] (HOLOTYPE: *B* destroyed, as photo F!, GH!; ISOTYPE: NY!).

Vernonia praecox (Kuntze) Schumann, Just's Bot. Jahresber. 26(1): 382. 1900.

Highly branched shrub up to 3 m tall; stems puberulent. Leaves cauline, subsessile to obviously petiolate; petioles 0.1 0.6 cm long; blades elliptic to narrowly elliptic or occasionally oblanceolate, 4–10 cm long, (0.5)1–3 cm wide, length/width ratio 3 5; essentially glabrous to puberulent, punctate-glandular and generally somewhat scabrous above, puberulent to tomentose (rarely essentially glabrous) and punctate-glandular below; acute to obtuse, occasionally with a mucronate tip, at the apex; cuneate to attenuate at the base; margins typically serrulate but may be serrate or entire. Inflorescences corymbose-paniculate. Heads with (10)11–15(17) florets; pedicels 1–5 mm long. Involucres turbinate, 9 14 mm tall; phyllaries 40–50, imbricate in 7 9 series, often with reduced bracts extending down the pedicel; inner phyllaries glabrous, usually thinly glandular

near the apex, often purple at the tip, 5–7.5 mm long, 1–1.8 mm wide, rounded to obtuse at the apex; outer phyllaries glabrous, 0.9–1.4 mm long, 0.5–1.1 mm wide, acute at the apex. Corollas purple, the tube 6 9 mm long, the lobes 3 4 mm long, the tube (1.75)2(2.3) times as long as the lobes. Anthers (3)3.5 4.7 mm long. Style branches 2.5–3.5 mm long. Pappus straw-colored; inner series of 45 -70 bristles (5.5)6 7.5(8) mm long; outer series (0.7)1 1.5 mm long. Achenes pubescent and glandular-dotted, (2)2.3 -3.3(3.7) mm long, 0.7–1 mm wide, length/width ratio 2–4.

Vernonia squamulosa is distributed from southern Bolivia south to the state of Catamarca in northwestern Argentina, occurring along the foothills of the Andes from 300–1800 m alt (Figure 3). It has also been reported from the state of La Rioja, Argentina by Cabrera (1944) but I have not seen a specimen from this state. Flowering occurs from July through November but mostly in August and September, varying with latitude and altitude. *Vernonia squamulosa* seems to prefer full sun or partial shade and has most often been collected on steep rocky sunny slopes with low shrub growth and occasionally from thickets and as an understory shrub. Its apparent affinities with *V. nitidula* are discussed with the latter species.

Representative specimens: **Bolivia:** DEPTO. SANTA CRUZ: Sierra de Santa Cruz, 1600 m, May, 1892, *Kuntze s.n.* (NY); Samaipata, Standort-Berghalde, campo, 1700 m alt., October 14, 1928, *J. Steinbach 8250* (G, MO, NY, S, UC); Camiri, Rio Parapeti oil refinery, hills covered with light, low, open woods, small shrub on sunny cliff, alt. 2500 ft, September 3, 1949, *W. M. A. Brooke 5572* (BM, NY); Camiri, Rio Parapeti oil refinery, start of pipeline, lat. 20°00′S, long. 63°15′W, alt. 2500 ft, on rocky slopes, September 3, 1949, *W. M. A. Brooke 5578* (BM). DEPTO. CHUQISACA: Rosal, lat. 19°30′S, long. 64°15′W, alt. 6000 ft, open rocky slopes, large shrub in wooded glen, September 30, 1949 [labeled as Depto. Cochabamba], *W. M. A. Brooke 5713* (BM, NY). **Argentina:** JUJUY: Depto. Capital, outlet of Laguna de Yala, 25 km NE of Jujuy, common, alt. 1500 m, September 26, 1938, *W. J. Eyerdam & A. A. Beetle 22208* (G, GH, MO, S, UC); Depto. Capital, Cerros near Jujuy, September 11, 1938, *Cabrera 4538* (GH, NY); Cedesma, Estacion, lagua, 600 m alt, September 3, 1927, *S. Venturi 5277* (GH, UC); SALTA: Oran, July, 1873, *P. G. Lorentz & G. Hieronymus 342* (G, NY); El Piquete, Lumbresas, August, 1904, *A. E. Ragonese 322* (SP); Rosario de la Frontera, June 14, 1933, *Cabrera 3131* (NY, SP); Cafayete, Cerro San Isidro, August 20, 1936, *Cabrera 3771* (NY, S, SP). CATAMARCA: Depto. Andalgala, September, 1915, *P. Jorgensen 1000* (GH, MO, UC); Depto. Ambato, entre Las Chacritas e Casa de Piedra, Ruta 62, lat. 27°40′S, long. 65°55′W, October 15, 1966, *O. Boelcke s.n.* (CTES); Depto. Capital, August 25, 1910, *Castillon s.n.* (GH). TUCUMAN: La Ramada, Burruyacu, September 18, 1913 *Peirano 9116* (GH); Depto. Capital, 480 m alt., September 15, 1908, *Lillo 8506* (A, GH, NY); Depto. Famailla, Quebrada de Lules, September 23, 1923, *S. Venturi 2559* (GH, UC); Santa Ana, November, 1902, *G. A. Baer 60* (S); Depto. Graneros, Dique de San Ignacio, July 31, 1968, *S. G. Tressens 70* (CTES, MO).

Vernonia series **Chamaedrys.** TYPE SPECIES: *Vernonia chamaedrys* Less.

Fruticose or suffrutescent perennials with a xylopodium; stems one to several, generally not highly branched below the inflorescence; leaves linear to ovate to oblanceolate; inflorescences thyrsoid-paniculate; heads with 4–25 florets, numerous, sessile to very short pedicellate; involucres turbinate to approaching campanulate.

Vernonia subseries **Laxae** Stutts. TYPE SPECIES: *Vernonia laxa* Gardner.

Inflorescences laxly thyrsoid-paniculate; heads with 10–15 florets. Otherwise having the general characters of the series.

4. *Vernonia viscidula* Less., Linnaea iv: 289. 1829. TYPE: BRAZIL. E. Brasilia tropica, *Sellow s.n.* (HOLOTYPE: not extant); NEOTYPE here designated: BRAZIL: Brasilia equinoctialis, *Sellow 776* (UC!).

Vernonia corymbulosa C. Martius ex Baker, Mart. Fl. Brasil. 6(2): 113. 1873. pro. syn. TYPE: BRAZIL: Minas Gerais, *C. Martius 744* (HOLOTYPE: M; ISOTYPES: BR(2)!).

Cacalia viscidula (Less.) Kuntze, Rev. Gen. Plant. 2: 971. 1891.

Suffrutescent perennial up to 2 m tall; stems ascending, viscid-pubescent. Leaves cauline, reduced upward, sessile to subsessile; blades normally elliptic but varying from obovate to ovate, (4.4)6–8(9) cm long, (1.5)2–3.5(4) cm wide, length/width ratio (2)2.5(3); scabrous above, tomentose below; acute at the apex; cuneate at the base; margins serrate to serrulate and slightly revolute. Inflorescences laxly thyrsoid-paniculate. Heads with 10–15 florets, subsessile to short pedicellate; pedicels 0.5–2(5) mm long. Involucres turbinate, 8–10 mm tall; phyllaries ca 30, imbricate in 5–6 series; inner phyllaries glabrous, often purple at the tip, 7 9.5 mm long, 1.5 1.8 mm wide, acuminate at the apex; outer phyllaries glabrous, 2–3.5 mm long, 0.7–1.2 mm wide, acute to acuminate at the apex. Corollas purple, the tube (4.5)5–6 mm long, the lobes 2.5–3(3.5) mm long, the tube ca. 2 times as long as the lobes. Anthers (2.2)3(3.2) mm long. Style branches 2.5–3 mm long. Pappus white; inner series of 40–50 bristles 5–6 mm long; outer series (0.6)0.8(1) mm long. Achenes pubescent and thinly glandular-dotted, (1.7)2(2.1) mm long, 0.8 1 mm wide, length/width ratio ca 2.

Vernonia viscidula is known only from a small area around the upper reaches of the Rio Velhas near Belo Horizonte, Minas Gerais,

Brazil, where it has been collected in campo and cerrado between ca 1200–1500 m alt. (Figure 4). Flowering occurs from April through June.

Vernonia viscidula can be distinguished from the closely related *V. laxa* by its viscid pubescence and the longer inner phyllaries (7 9.5 mm vs 4 4.5 mm) which are acuminate (vs. obtuse) and not glandular at the apex.

The Sellow specimen designated here as the neotype appears to have been annotated by Lessing and therefore would be preferable to other available specimens which may or may not have been seen by the original author. Baker (1873) listed several specimens as representative but did not designate a type. However, Baker labeled a specimen (*P. Claussen s.n.*) now located at Kew as a type for *V. viscidula*. This and other types for valid species designated but never published by Baker are not considered valid types because they were selected in an arbitrary manner, often without regard to the work of previous authors.

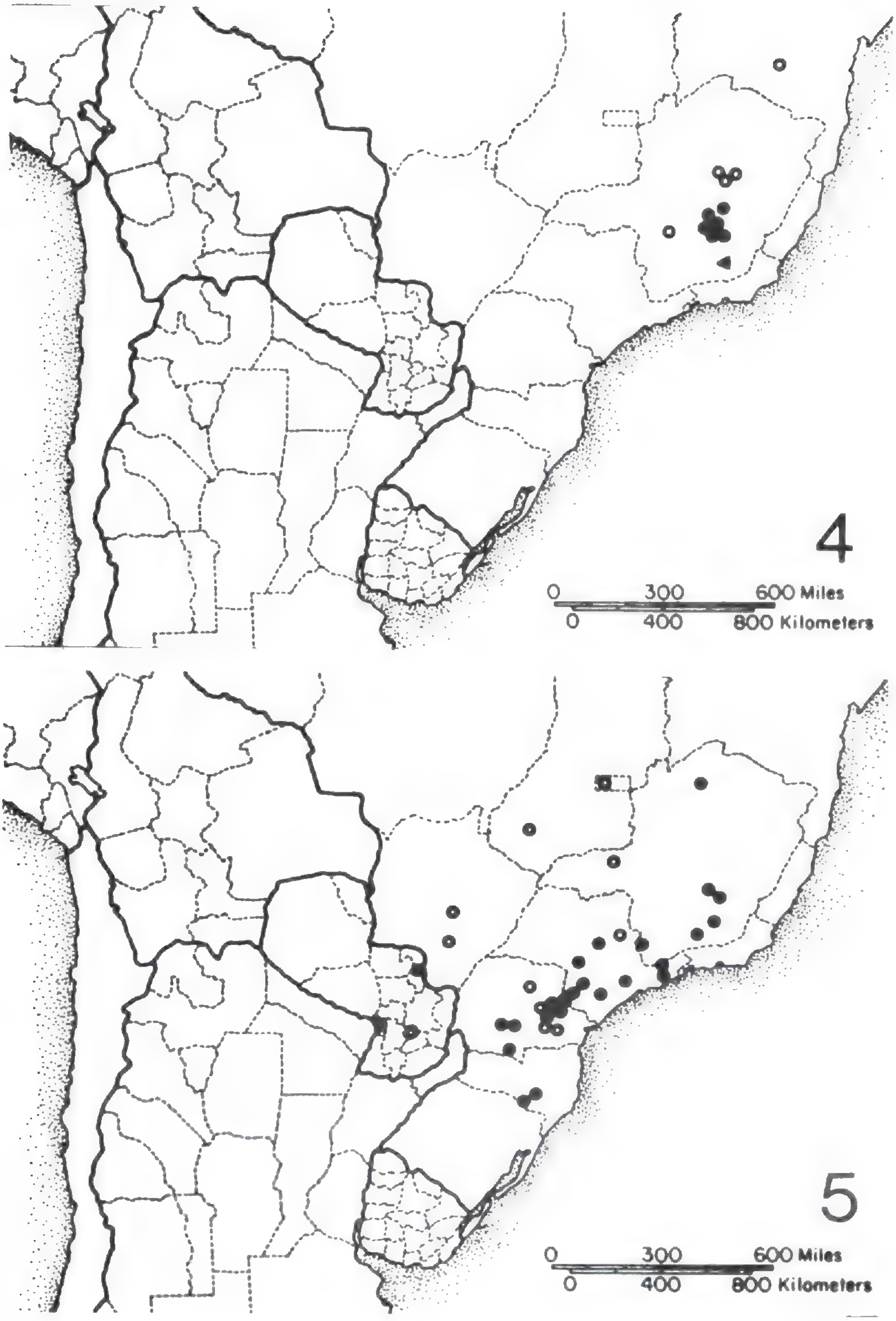
REPRESENTATIVE SPECIMENS: **Brazil.** MINAS GERAIS: Mun. Nova Lima, Pico de Belo Horizonte, campo, 1300 m alt., June 6, 1945, *L. O. Williams & V. Assis 7139* (GH, RB, UC); Mun. Nova Lima, Serra da Mutuca, near Belo Horizonte, 12–1400 m alt., April 7, 1945, *L. O. Williams & V. Assis 6592* (GH); Mun. Belo Horizonte, Barreiro, campo, April 19, 1935, *Mello-Barreto 1351* (RB); Mun. Serra do Cipó, June 21, 1964, *A. P. Duarte 8103* (RB); Itabirito, 40 km S of Belo Horizonte, cerrado, June 18, 1964, *J. M. Pires 56938* (GH, NY, US); Serra do Taquaril, cerrado, May 19, 1933, *Mello-Barreto 4233* (SP); In campis and caxoeira do campo, 1839, *P. Claussen 50* (G); Cachoeira do campo, 1857, *Casaretto 2747* (G); 1840, *P. Claussen 509A* (BR); *P. Claussen s.n.* (K -as photos GH, NY).

5. *Vernonia elsieae* Stutts, Brittonia 35(4): 351–352. 1983.

Vernonia rigiophylla Schultz-Bip. ex Baker, Mart. Fl. Brasil. 6(2): 118. 1873; non *V. rigiophylla* DC., Prodromus 5: 15. 1836. LECTOTYPE: BRAZIL: In campis prope Sta. Anna, *Lund s.n.* (C!).

Cacalia rigiophylla (Schultz-Bip. ex Baker) Kuntze, Rev. Gen. Bot. 2: 971. 1891.

Fruticose perennial up to ca. 1 m tall; stems ascending. Leaves cauline, slightly reduced upward, sessile; blades linear, 2–5 cm long, 0.2 0.4 cm wide, length/width ratio 10 15; strigose-pubescent above, sometimes becoming nearly glabrous with age; densely strigose-pubescent below; acute at the apex; cuneate to attenuate at the base; margins entire and revolute. Inflorescences laxly thyrsoid-paniculate. Heads with 10–12 florets, sessile to short pedicellate; pedicels 0.1 2(4) mm long. Involucres turbinate, 8–10 mm tall; phyllaries ca 30, imbricate in 6–7 series; inner phyllaries glabrous, 4.5–5 mm long, 1.1–1.4 mm wide, acute to obtuse at the apex; outer



Figures 4 and 5. Distribution of *Vernonia* subsect. *Chamaedrys* in southern South America. **4.** *V. viscidula* (●), *V. laxa* (o) and *V. elsieae* (▲). **5.** *V. mucronulata* (●) and *V. cuneifolia* (o).

phyllaries glabrous, 1 -1.2 mm long, 0.7 -0.8 mm wide, acute to short acuminate at the apex. Corollas purple, the tube 5–5.5 mm long, the lobes 2–2.2 mm long, the tube ca 2.5 times as long as the lobes. Anthers 3–3.5 mm long. Style branches 2–2.2 mm long. Pappus off-white or pale tan; inner series of ca. 40 bristles 5–6 mm long; outer series 0.5–1 mm long. Achenes pubescent and densely glandular-dotted, (2)2.5(2.7) mm long, 0.8–1 mm wide, length/width ratio ca. 2.5.

Vernonia elsieae is known from a few collections from the early 1800's in the states of Goias and Minas Gerais, Brazil (Figure 4). Flowering and fruiting seem to be centered around August.

Possible explanations for the apparent absence of modern collections are that the species is no longer extant or that it is very rare and has simply been overlooked. Several of the species in this subsection seem to be restricted to specific habitats and are virtually impossible to find when not in flower. Narrow-leaved forms of *V. crassa* are often misidentified as this species (Stutts, 1983).

REPRESENTATIVE SPECIMENS: **Brazil:** *Riedel s.n.* (NY); *Riedel 256* (G). GOIÁS: St. Anna, August, 1834, *Riedel s.n.* (US). MINAS GERAIS: *Glaziou 17070* (as photos GH, NY); Barbacena, August, 1824 *Riedel s.n.* (GH). Serra de São João del Rei, June, 1896, *Alvaro Silveira 1257* (RB).

6. *Vernonia laxa* Gardner, Hook. Lond. Journ. Bot. 5: 214. 1846.
TYPE: BRAZIL: MINAS GERAIS, near Formigas, in the sertao, July, 1840, *Gardner 4802* (HOLOTYPE: BM!; ISOTYPES: B as photos F!, GH!, NY!, F (fragment)!, G!, K—as photo GH!).

Cacalia laxa (Gardner) Kuntze, Rev. Gen. Plant. 2: 970. 1891.

Suffrutescent perennial up to 1.5 m tall; stems ascending. Leaves cauline, few in number, reduced upward, subsessile; petioles 0.1–0.3 cm long; blades elliptic to oblanceolate, 5–8.5 cm long, (1.5)2–3.5(4) cm wide, length/width ratio 2 -3; scabrous above; densely tomentose below; acute at the apex; cuneate at the base; margins serrate to subserrate and slightly revolute. Inflorescences laxly thyrsoid-paniculate. Heads with 10–15 florets, sessile. Involucres turbinate 6–6.5 mm tall; phyllaries ca 30, imbricate in 5–6 series; inner phyllaries glandular near the apex and often purple at the tip, 4–4.5 mm long, 1.2–1.4 mm wide, obtuse at the apex; outer phyllaries glabrous, 1.1–1.8 mm long, 0.7–1.1 mm wide, acute at the apex. Corollas purple, fading to white, the tube 3.6 -4.2 mm long, the lobes 2.1–2.3 mm long, the tube ca 1.75 times as long as the lobes. Anthers ca 2.2 mm long. Style branches ca. 2 mm long. Pappus pale tan;

inner series of 40–50 bristles 4.5–5.5 mm long; outer series 0.5–0.8 mm long. Achenes thinly pubescent and glandular-dotted, 2.5–3 mm long, 0.8–1 mm wide, length/width ratio ca. 3.

Vernonia laxa is known only from a few collections in the states of Minas Gerais and Bahia, Brazil where it is apparently numerous to common in scattered localized areas of campo rupestre or similar habitats around 1200–1400 m alt. (Figure 4). Flowering occurs from May through July. *Vernonia laxa* is most closely related to *V. viscidula* from which it can be distinguished as indicated above.

REPRESENTATIVE SPECIMENS: **Brazil:** BAHIA: Mun. de Rio de Contas, base de Pico das Almas, 18 km NW de Rio de Cantas, alt. ca 1300 m, common, July 22, 1979, *King, Mori, Santos & Hage 8105* (M). MINAS GERAIS: Mun. Diamantina, Diamantina, June 5, 1955, *E. Pereira 1692* (M, RB); Mun. Diamantina, ca 15 km NW of Diamantina, campo rupestre, alt. ca. 1400 m, common, October 4, 1980, *Stutts 935* (GA); Mun. Diamantina, June, 1934, *A. C. Brade 10568* (RB); Mun. Belo Horizonte, Parque Vera Cruz, *Mello-Barreto 8380* (F).

Vernonia subseries **Chamaedrys.** TYPE SPECIES: *Vernonia chamaedrys* Less.

Inflorescences densely thyrsoid-paniculate; heads with 4–25 florets. Otherwise having the general characters of the series.

7. *Vernonia chamaedrys* Less., Linnaea iv: 259–260. 1829. TYPE: BRAZIL: E. Brasilia tropica, *Sellow s.n.* (HOLOTYPE: not extant); LECTOTYPE here designated: ISOTYPE at G-DC, as IDC microfiche!).

Cacalia chamaedrys (Less.) Kuntze, Rev. Gen. Plant. 2: 969. 1891.

Vernonia ilex Chodat, Bull. Herb. Boissier, Ser. II, 4: 410. 1902. TYPE: LECTOTYPE selected from among syntypes: PARAGUAY: *Hassler 1708* (G!: ISOLECTOTYPES: G!, G-DEL—as photo F!, NY!).

Suffrutescent perennial up to 1.2 m tall; stems ascending, whitish pubescent. Leaves cauline, reduced upwards, sessile; blades elliptic to obovate, 2.5–6 cm long, 1.5–2.5 cm wide, length/width ratio (1.5)2(3.5); punctate-glandular above; white to greyish tomentose below; acute to acuminate at the apex; rounded to cordate at the base, rarely cuneate; margins serrate to serrulate or dentate. Inflorescences densely thyrsoid-paniculate. Heads with (8)10–13(16) florets, sessile. Involucres turbinate, (5)6–8(9) mm tall; phyllaries ca. 30–35, imbricate in 6–7 series; inner phyllaries glandular near the apex and often purple at the tip, occasionally thinly pubescent, (4.5)5–6(6.5) mm long, 0.6–1.4 mm wide, acute to obtuse or occasionally rounded at the apex; outer phyllaries normally pubescent,

1–2 mm long, 0.5–1 mm wide, acute to acuminate at the apex. Corollas purple, fading to white, sweet-scented, the tube ca 1.5 times as long as the lobes. Anthers 3–4 mm long. Style branches ca 2–3 mm long, often purple. Pappus white to pale tan; inner series of 50–60 bristles (4.5)5.5–6(7) mm long; outer series 0.5–1.2 mm long. Achenes thinly pubescent and glandular-dotted, 3 4 mm long, 0.9–1.1 mm wide, length/width ratio 3–4.

Vernonia chamaedrys occurs in full sun in campo and disturbed grassland habitats, often forming large, widely scattered populations. The species is centered in southern Paraguay and northern Argentina and extends eastward and northward from Rio Grande do Sul, Brazil to São Paulo and Mato Grosso do Sul, Brazil (Figure 2). I have only seen one specimen, without a specific locality mentioned, labeled as collected in Minas Gerais, Brazil (Capanema 4902-RB). Flowering occurs from January through March.

Vernonia chamaedrys can be distinguished from the closely related species *V. mucronulata* and *V. cuneifolia* by its larger achenes (3–4 mm vs 2–2.5(2.8) mm) and its sessile heads.

The specimen chosen as the lectotype is the only known extant isotype of the original Sellow collection. This specimen, deposited at G-DC, bears the annotation "E. Brasilia tropica" just as listed by Lessing in the original publication. The specimen also bears the name Sellow but does not have a collection number. This same specimen is cited by de Candolle in his treatment of *Vernonia* (Candolle, A. P. de, 1836). In the past some workers have apparently considered a specimen of *Sellow 3653* deposited at B (no longer extant) as the type for this species. Photographs of *Sellow 3653* (F, GH, NY) show that it was labeled as collected in "Brasilia meridionalis" and was annotated as "Ex reliquis Sellowianis, Humboldt, Dec. 1836" and "Ex herb. Kunth". It is therefore highly improbable that *Sellow 3653* is the collection on which Lessing based the species, whereas the specimen at G-DC certainly is an isotype and should serve as the lectotype.

Representative specimens: **Brazil:** MATO GROSSO DO SUL: Mun. Ponta Pora, 22 km from Ponto Pora toward Bela Vista, in campo, February 19, 1968, *A. Krapovickas et al. 14061* (CTES); Entre Dourados e Ponta Pora, campo limpo, February 5, 1952, *M. Kuhlmann s.n.* (SP); Mun. de Maracaju, Fazenda Santa Cruz, cerrado, *D. Sucre 10577* (GA, RB). MINAS GERAIS: Without locality, *Capanema 4902* (RB). PARANÁ: BR 277, 28 km W of Guarapuava, disturbed campo, February 22, 1982, *Stutts 1227* (GA, MBM) SANTA CATARINA: Mun. Campos Novos, Maromba, February 26, 1964, *A. Castellanos 24583* (RB); Curitibanos, alt. 900 m, February 22, 1962, *P. Reitz & R. M. Klein 12206* (BR, G, NY, RB, US). RIO GRANDE

DO SUL: Entre S. João Mirim e Carajazinho, em touceiras, campo, January 27, 1964, *E. Pereira 8641 & G. Pabst 7916* (GA, LP, M, RB); Mun. Julio de Castilhos, March 4, 1948, *Palacios-Cuezzo 2583* (RB). **Paraguay:** DEPTO. SAN PEDRO: Alto Paraguay, Primavera, February 7, 1956, *A. L. Woolston 645* (GH, NY, S, US); Rio Tapiracuay, 8 km dè San Estanislao, camino Rosario, February 17, 1968, *A. Krapovickas et al 13946* (CTES, LP). DEPTO. CENTRAL: Itá, Orilla del Arroyo Lazarillo, campo bajo, January 29, 1966, *A. Krapovickas et al. 12130* (CTES, M, US). DEPTO. PARAGUARI: Tapé Guazú, entre Quyndy y Caápuaí, campo alto abiento, March, 1971, *A. Schinini 4300* (CTES). DEPTO. GUAIRA: Villarrica, very common in the campo, January, 1929, *P. Jorgensen 3514* (A, GH, MO, NY, S, US). DEPTO. MISIONES: Santiago, Estancia La Soledad, extremely common, February 7, 1955, *T. M. Pedersen 3293* (BR, G, MO, S). **Argentina:** FORMOSA: Laishi, grandes matas, March, 1918, *P. Jorgensen 2017* (GH, SP, UC). PILCOMAYO: Ruta 11 near Los Blancas, March 18, 1947, *Ismael Morel 189* (RB). CHACO: Los Brenas, campos, 250 m alt., November 12, 1929, *S. Venturi 9791* (BM, GH, MO, NY, S). SANTA FE: Arroyo Pindo cerca de Villa Ocampo, February 12, 1946, *Hayward s.n.* (BM). CORRIENTES: Depto. Mburucuya, Estancia Santa Teresa, February 24, 1951, *T. M. Pedersen 1029* (BR, GH, MO, S); Santo Tomé, San Mateo, January 29, 1947, *Huidobro 4622* (GH, MO, NY, UC). MISIONES: Santa Ana, March 3, 1910, *Rodriguez 175* (A, GH, NY). ENTRE RIOS: Depto. La Paz, Montes del Rio Guayquiraró, La Morenita, January 23, 1960, *A. Burkart 21492* (UC).

8. *Vernonia mucronulata* Less., Linnaea iv: 266. 1829. TYPE: BRAZIL: E. Brasilia tropica misit, *Sellow s.n.* (HOLOTYPE: not extant). NEOTYPE here designated: BRAZIL: *Sellow s.n.* (P—as photo F!).

Vernonia collina Gardner, Hook. Lond. Journ. Bot. 5: 213. 1846. TYPE: LECTOTYPE selected from among syntypes: BRAZIL: Minas Gerais, open hilly places near Morro Velho, September, 1840, *Gardner 4801* (BM!; ISOLECTOTYPE: K as photo GH!, as photo NY!).

Vernonia moquinioides C. Martius ex Baker, Mart. Fl. Brasil 6(2): 116. 1873. *pro. syn.*

Cacalia mucronulata (Less.) Kuntze, Rev. Gen. Plant. 2: 970. 1891.

Fruticose perennial 0.5–1.5 m tall; stems ascending, upper portions ferruginose- or whitish-tomentose. Leaves cauline, somewhat reduced upwards, subsessile; petioles 0.1 0.4 cm long; blades typically elliptic, varying from ovate to rarely oblanceolate, 3 6 cm long, 1.5–3 cm wide, length/width ratio ca 2; glabrous and punctate-glandular above; densely ferruginose to grey tomentose below; mucronate at the apex; cordate to rounded at the base, rarely cuneate, upper leaves and bracts of inflorescences never cuneate; margins crenate-serrulate with mucronate-tipped segments or entire, slightly revolute. Inflorescences densely thyrsoid-paniculate. Heads with (5)6–10(11) florets, subsessile to sessile; pedicels up to 3 mm long. Involucres turbinate, (6)7–8(9.5) mm tall; phyllaries ca (30)40 45,

imbricate in 6 7 series; inner phyllaries thinly glandular near the apex and occasionally purple at the tip, occasionally thinly pubescent near the margins, 4.5 6 mm long, 0.6 1.4 mm wide, acute at the apex; outer phyllaries glabrous or thinly pubescent near the margins, 1–2 mm long, 0.5–1 mm wide, acute at the apex. Corollas purple, fading to white, the tube 4.5 5.5 mm long, the lobes 2.5–3.5 mm long, the tube ca 1.6 times as long as the lobes. Anthers ca 3 mm long. Style branches 2 3 mm long. Pappus pale tan to white; inner series of 35–65 bristles 4.5–6.5 mm long; outer series 0.4–1 mm long. Achenes thinly pubescent and glandular-dotted, 2 2.5(2.8) mm long, 0.6–0.8 mm wide, length/width ratio 2.5–3.5.

Vernonia mucronulata is apparently tolerant of a wide range of conditions being found in dry open sites and in moist, partially shaded areas in both campo and cerrado in southeastern Brazil (Figure 5). Flowering occurs from July through November.

Vernonia mucronulata is most often confused with *V. cuneifolia* from which it may be distinguished by having leaves elliptic, occasionally ovate to oblanceolate, the lower leaves cordate to rounded, occasionally cuneate at the base, the upper most leaves and bracts of the inflorescence cordate to rounded at the apex, and the inner phyllaries acute at the apex, while *V. cuneifolia* has leaves obovate, all leaves and bracts of the inflorescence cuneate at the base, leaves obtuse to rounded at the apex and phyllaries rounded to obtuse at the apex.

The chosen neotype agrees with time and place of collection cited in the original treatment.

Representative specimens: **Brazil:** MINAS GERAIS: Morro Velho, September, 1840, *Gardner 4800* (BM); Morro de Pedras, near Belo Horizonte, 1035 m alt., in campo, July 28, 1945, *L. O. Williams & V. Assis 8025* (BM, BR, F, G, GA, GH, MO, NY, RB, S, UC); Ouro Preto, in capoeiras, September 7, 1952, *A. Macêdo 3789* (MO, S); Barbacena, campo, 1879, *Glaziou 11074* (S); Mun. Andrelandia, Cruz das Almas, campo, very frequent, August 23, 1936, *Mello-Barreto 5231* (F); Caldas, *A. F. Regnell II 141* (BR, F, M, NY, S). SÃO PAULO: Mun. São Carlos, 4.5 km N of São Carlos, August 5, 1961, *J. M. de Freitas Campos 7* (US); Mun. Botucatu, 3 km da rodavia Castelo Branco, cerrado, September 11, 1973, *Maria Sakane 66* (SP); Mun. de Sorocaba, nativa a beira da estrada para Itú, July 22, 1968, *H. F. L. Filho 456* (CTES, LP); Campos de Jordao, September, 1945, *J. E. Leite 4023* (US); Mun. São José dos Campos, small area of disjunct cerrado 7 km SE of São José dos Campos, July 20, 1962, *I. Mimura 458* (NY, RB); Mun. Itararé, Rio Verde, cerrado, February 17, 1982, *Stutts 1226* (GA, MBM); Mun. Itararé, Fazenda Esplanada, campocerrado intermediate, alt. 950 m, February 17, 1982, *Stutts 1217* (GA, MBM); Mun. Itapetininga, campo, September 28, 1959, *S. M. de Campos 13* (GA, RB). PARANÁ: Mun. Sengés, PR 151, 5 km N of Sengés, Rio Pelame, grazed campo, numerous, all vegetative, February 17, 1982, *Stutts 1212* (GA, MBM); Mun. Jaguariaiva, campo, July

16, 1915, *P. Dusen 17087* (F, G, GH, MO, S); Mun. Castro, 15 km N of Castro, campo, in bud, February 15, 1982, *Stutts 1187* (GA); Mun. Ponta Grossa, entre Ponta Grossa e Castro, campo alto, August 3, 1960, *A. P. Duarte 5375* (GA, RB); Mun. Guarapuava, Fazenda São Pedro, BR 373, 20 km S of BB 277, February 25, 1982, *Stutts 1246* (GA, MBM); Mun. Lagoa Seca, BR 277, 6 km E of Lagua Seca, pasture, October 27, 1980, *Stutts 1015* (GA, MBM); Mun. Palmas, just E of Palmas on BR 280, ca. 56 km W of BR 476, campo, February 26, 1982, *Stutts 1254* (GA, MBM). SANTA CATARINA: Mun. Lajes, Passo do Socorro, campo, 900 m alt., November 1, 1963, *R. M. Klein 4451* (LP, RB); Mun. Lajes, Ipema, campo, 800 m alt., September 14, 1963, *P. Reitz & R. M. Klein 16296* (LP, RB).

9. *Vernonia cuneifolia* Gardner, Hook. Lound. Journ. Bot. V: 215. 1846. TYPE: BRAZIL: Minas Gerais, in a marsh on the Serra das Araras on the western confines of the province of Minas Gerais, June, 1840, *Gardner 4778* (HOLOTYPE: BM!).

Vernonia pohliana Schultz-Bip. ex Baker, Mart. Flora. Brasil. 6(2): 113. 1873. *pro. syn.*

Cacalia cuneifolia (Gardner) Kuntze, Rev. Gen. Plant. 2: 969–970. 1891.

Vernonia itapensis Chodat, Bull. Herb. Boissier, Ser. II, 2: 301–302. 1902. TYPE: LECTOTYPE selected from among syntypes: PARAGUAY: Cerro Largo, Sera Maracayú, in campo prope Ipé-hu (Ypé-Jhu), October, 1898, *Hassler 5142* (NY!; ISOLECTOTYPES: BM!, G!, GH!, UC!).

Suffrutescent perennial up to 1.5 m tall; stems ascending, ferruginose-tomentose. Leaves cauline, reduced upwards, sessile to subsessile; blades obovate, (3)3.5–5.5(6.5) cm long, 1.5 2.5 cm wide, length/ width ratio (1.7)2(4); glabrous and thinly punctate-glandular above; ferruginose-tomentose below; obtuse to rounded at the apex; cuneate at the base; margins serrulate to serrate, occasionally crenate-serrulate near the apex, the serrations often with mucronate-tipped segments, slightly revolute. Inflorescences densely thyrsoid-paniculate. Heads with (7)10–12(15) florets, short pedicellate to subsessile; pedicels up to 3 mm long. Involucres turbinate (6.5) 7.5–9(9.5) mm tall; phyllaries ca 30–35(45), imbricate in 6–7 series with additional reduced bracts often extending down the pedicel; inner phyllaries thinly glandular near the apex and normally purple at the tip, occasionally thinly pubescent near the margins, (5)5.5(6.5) mm long, (0.9)1.2(1.6) wide, rounded to obtuse at the apex; outer phyllaries glabrous or thinly pubescent near the margins, (1)1.2(1.5) mm long, 0.6–0.9(1.2) mm wide, acute at the apex. Corollas purple, fading to white, the tube 4–5.7 mm long, the lobes 2.2–3.2 mm long, the tube ca 1.8 times as long as the lobes. Anthers 3–3.2 mm long. Style branches 2–2.5 mm long. Pappus white to pale tan; inner series of 30–40 bristles 5–6.5 mm long; outer series 0.4–0.8(1) mm long.

Achenes glabrous to thinly pubescent, densely glandular-dotted, 2–2.5(2.8) mm long, 0.6–0.8 mm wide, length/width ratio 2.5–3.5.

Vernonia cuneifolia is most often found in moist areas but may also occur in relatively dry, open sites such as overgrazed cattle pasture. It occurs naturally in both campo and cerrado habitats in southeastern Brazil and Paraguay (Figure 5). Plants from the western portion of the species range tend to have thinly pubescent achenes. Flowering occurs from May through August.

In addition to confusion with *V. mucronulata,* this species may also be confused with vegetative specimens of *V. oligactoides* Less. but is easily distinguished when flowering.

REPRESENTATIVE SPECIMENS: **Brazil:** GOIAS: Mun. Jataí, sub-arbusto da vargem, July 18, 1951, *A. Macêdo 3317* (RB); Marécaga du Rio Gama, 1896, *Glaziou 21638* (NY, S). DISTRITO FEDERAL: Côrrego Samambaia, near Taguatinga, 20 km W of Brasilia, cerrado, 1000 m alt., July 13, 1966, *H. S. Irwin et al 18199* (MBM, US). MATO GROSSO DO SUL: Sidrolandia, July 12, 1969, *Hatschbach 21787* (MBM, NY, UC); Mun. Rio Brilhante, Rio Sta. Luzia, August 31, 1973, *Hatschbach 32514* (MBM). MINAS GERAIS: Mun. Uberlandia, Rio Uberlandia, cerrado, July 22, 1956, *A. Macêdo 4563* (RB). SÃO PAULO: Between São Simão and Casa Branca, July, 1855, *A. F. Regnell III–1779* (S). PARANÁ: Mun. São Jeronimo do Serra, Fazenda NhoÓ, September 27, 1970, *Hatschbach 24794* (MBM); Mun. Ponta Grossa, Rio Botuguara, BR 376, campo, March 6, 1982, *Stutts 1298* (GA, MBM); Mun. Porto Amazonas, June 10, 1914, *P. Dusen 15160* (S); Rio Tibagi, sandstone bank, June 24, 1967, *J. L. Lindemann & J. H. Haas 5537* (NY). **Paraguay:** DEPTO. AMAMBAY: Sierra de Amambay, 1907–08, *Hassler 10464* (G, NY, UC). DEPTO. LA CORDILLERA: Region of Lake Ypacarai, July, 1913, *Hassler 11850* (BM, G, GH, NY, UC, US). DEPTO. GUAIRA: Villarrica, common in meadows, July, 1930, *P. Jorgensen 4431* (F, GH, MO, NY, S).

10. *Vernonia oligactoides* Less., Linnaea vi: 648. 1831. TYPE: BRAZIL: *Sellow s.n.* (HOLOTYPE: not extant). NEOTYPE here designated: BRAZIL: Estado do São Paulo, Mun. Itararé, Fazenda Esplanada, habitat campo-cerrado intermediate, February 17, 1982, *Stutts 1214* (GA!).

Vernonia sorocabae Schultz-Bip. ex Baker, Mart. Fl. Brasil. 6(2): 58. 1873. pro. syn.

Cacalia oligactoides (Less.) Kuntze, Rev. Gen. Plant. 2: 970. 1891.

Vernonia conyzoides Chodat, Plantae Hasslerianae I: 143. 1901. TYPE: PARAGUAY: In uliginosis Ipé-hu (Ypé-Jhu), Sierra Maracayu, November, 1898, *Hassler 5289* (HOLOTYPE: G; ISOTYPE: G!).

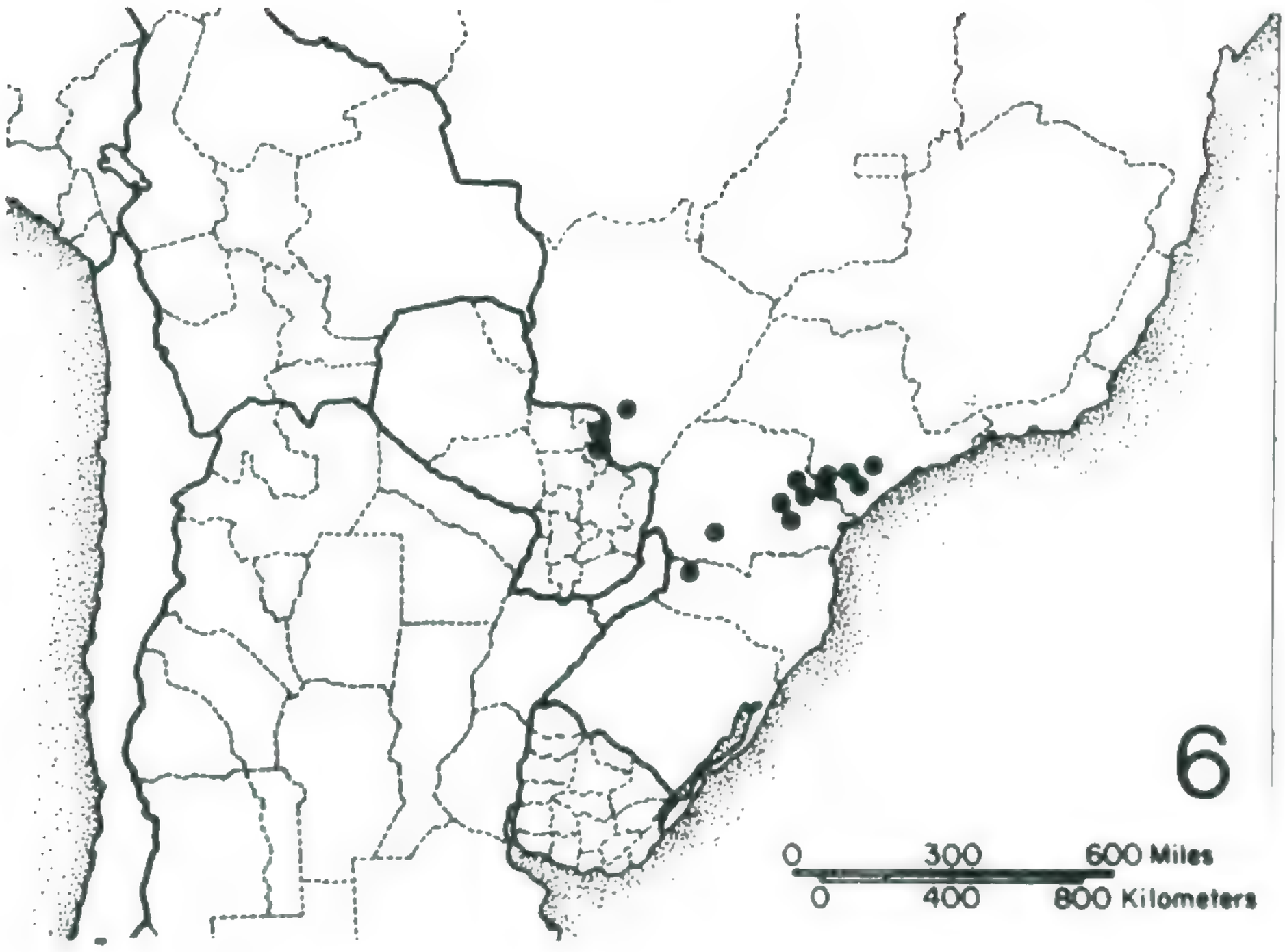
Suffrutescent perennial up to 2 m tall; stems ascending, densely yellowish-brown lanuginose. Leaves cauline, reduced upwards, sessile or the lower leaves subsessile to short petiolate; petioles up to 0.4 cm long; blades oblanceolate or the upper leaves occasionally

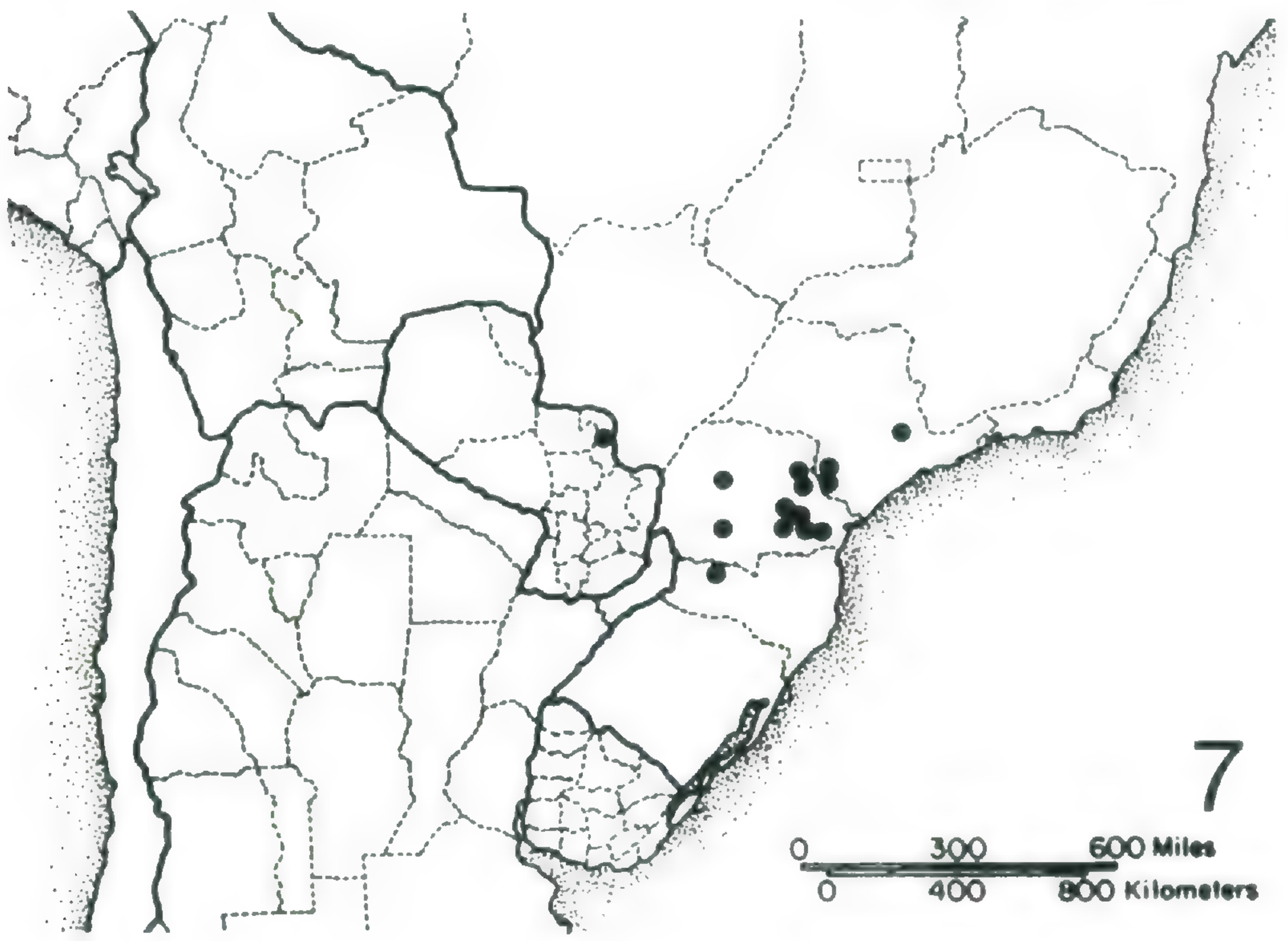
obovate, (7.5)10–15(20) cm long, (2.5)3–5(6) cm wide, length/width ratio (2.5)3.5(4.5); deep green, glabrous and thinly punctate-glandular above; yellowish-brown lanuginose below; acute to obtuse at the apex; cuneate to attenuate at the base; margins serrulate to occasionally serrate, crenate or entire, slightly revolute. Inflorescences densely thyrsoid-paniculate. Heads with (15)20–25 florets, sessile. Involucres more or less turbinate but having some tendency towards campanulate, (7)8 10(13) mm tall; phyllaries 35–50, imbricate in 7–9 series; inner phyllaries lanuginose on exposed dorsal portion, (5)6(7.5) mm long, (1)1.4(2) mm wide, acute to obtuse at the apex; outer phyllaries lanuginose on exposed dorsal portion, 2–3 mm long, 1–1.5 mm wide, acute at the apex. Corollas rosy-purple, fading to pale purple, the tube 6 8.5 mm long, the lobes 3.2–4.5 mm long, the tube ca 2 times as long as the lobes. Anthers 3.5 4.2 mm long. Style branches 3 4 mm long, often purple. Pappus white to pale tan; inner series of 50-65 bristles 6–7.5 mm long; outer series (0.6)0.8(1.3) mm long. Achenes pubescent and glandular-dotted, 3.2 4.5 mm long, 0.8-1.1 mm wide, length/width ratio ca. 4.

Vernonia oligactoides occurs in full sun on dry sites in campo and cerrado vegetation, with a discontinuous distribution on the southern Brazilian planalto from northwestern Santa Catarina to southern São Paulo, Brazil and westward to eastern Paraguay and southern Mato Grosso do Sul, Brazil (Figure 6). Flowering occurs from February through May.

Vernonia oligactoides is occasionally confused with *V. cuneifolia* or *V. mucronulata* from which it differs in several characters.

REPRESENTATIVE SPECIMENS: **Brazil:** MATO GROSSO DO SUL: Entre Dourados e Ponta Porã, campo limpo, February 5, 1952, *E. Kuhlmann s.n.* (SP). SÃO PAULO: In campos near Sorocaba, February, 1834, *Lund s.n.* (NY, US); Mun. de Itapetininga, rodovia Raposo Tavares, km 150, cerrado queimado e cortado, July 17, 1962, *M. S. Labouriau 129* (SP); Mun. Itapetininga, Fazenda Sta. Luzia do Campo Largo, SSE da cid. de Itapetininga cerrado, March 17, 1960, *S. M. de Campos 208* (SP); Mun. Itararé, near border with Mun. Itaberé, Rio Verde, edge of cerrado, February 17, 1982, *Stutts 1225* (GA); Mun. Itararé, campo, April 16, 1910, *P. Dusen 9680* (BM, NY, S). PARANÁ: Mun. Arapoti, ca. 4 km N of Arapoti, PR 092, campo, February 16, 1982, *Stutts 1206* (GA): Mun. Jaguariaiva, April 12, 1910, *P. Dusen 9626* (G, GH, M, S); Mun. Tibagi, campo, 732 m alt., April 10, 1959, *Hatschbach 5607* (HBR); Mun. Ponta Grossa, campo, March 29, 1904, *P. Dusen 4304* (A, MO, S); Mun. Laranjeiras do Sul, nos arredores da cidade, campo, May 1, 1957, *Hatschbach 3876* (HBR, MBM, R). SANTA CATARINA: Mun. Campo Eré, Fazenda Campo São Vicente, campo, 900 m alt., February 29, 1964, *R. M. Klein 5033* (HBR, LP). **Paraguay:** DEPTO. AMAMBAY: Capubarý, March 16, 1951, *G. J. Schwarz 12177* (US); Serra de Amambay, estrella, campo, February, 1908, *T. Rojas 10186* (BM, G, GH, MO, NY, S, UC).





Figures 6 and 7. Distribution of *Vernonia* subsect. *Chamaedrys* in southern South America. **6.** *V. oligactoides* (●). **7.** *V. oligolepis* (●).

11. *Vernonia oligolepis* Schultz-Bip. ex Baker, Mart. Fl. Brasil. 6(2): 56–57. 1873. TYPE: BRAZIL: Habitat in Brasilia centrali, *Riedel 1171* (HOLOTYPE: K!; ISOTYPES: F—as fragment !, P, US!).

Cacalia oligolepis (Schultz-Bip. ex Baker) Kuntze, Rev. Gen. Plant. 2: 970. 1891.

Fruticose perennial up to 1.5 m tall; stems typically with numerous lateral branchlets, puberulent. Leaves cauline, somewhat reduced upwards, subsessile to sessile; petioles 0.1–0.2 cm long; blades linear-lanceolate, (2.5)3–6(8) cm long, (0.3)0.4–0.7(0.9) cm wide, length/width ratio (5)8(17); glabrous and punctate-glandular above; thinly strigose and punctate-glandular below; acute at the apex; rounded at the base; margins entire, slightly revolute. Inflorescences densely thyrsoid-paniculate. Heads with (4)5(6) florets, subsessile to sessile; pedicels up to 2 mm long. Involucres turbinate, (6)6.5–8(8.5) mm tall; phyllaries ca 16–20, imbricate in 4–5 series; inner phyllaries sericeous to glabrous on exposed dorsal portion, (4.7)5–6(6.5) mm long, (1)1.5–1.6(1.9) mm wide, acute to obtuse at the apex; outer phyllaries sericeous to glabrous on the exposed dorsal portion, 1–1.9 mm long, 0.6–1 mm wide, acute to obtuse at the apex. Corollas light purple, fading to white, the tube 4.5–6 mm long, the lobes (3.2)3.5–4.5(4.7) mm long, the tube ca 1.4 times as long as the lobes. Anthers 3.5–4.2 mm long. Style branches (2.7)3–3.2(4) mm long. Pappus white; inner series of 75–100 bristles 7–8.5 mm long; outer series (0.5)1(2) mm long. Achenes pubescent and glandular-dotted, 3–4 mm long, 0.8–1 mm wide, length/width ratio 3–4.

Vernonia oligolepis occurs in full sun in campo and campo-cerrado habitats, with a discontinuous distribution on the southern Brazilian planalto from northern Santa Catarina north to São Paulo, Brazil and west to northern Paraguay (Figure 7). Flowering occurs from December through March.

Vernonia oligolepis is seldom confused with other species but may occasionally be misidentified as *V. lucida* Less. from which it differs in the leaves and the number of florets per head (margins entire vs serrulate; (4)5(6) florets vs (8)10–12(13) florets).

REPRESENTATIVE SPECIMENS: **Brazil:** SÃO PAULO: Limeira, *J. I. de Lima s.n.* (R, RB); Mun. Itapetininga, 10 km NE da vila de Alambari, km 145 na estrada São Paulo-Itapetininga, campo, January 23, 1969, *S. M. de Campos 172* (G, R, RB); Mun. Itararé, Rio Verde, margin of cerrado, February 17, 1982, *Stutts 1223* (GA); Mun. Itararé, Fazenda Esplanada, campo-cerrado intermediate, 950 m alt., February 17, 1982, *Stutts 1215* (GA). PARANÁ: Mun. Campo Mourão, Campo Mourao, Febru-

ary 2, 1962, *Hatschbach 8843* (MBM); Mun. Arapoti, 4 km N Arapoti, campo, February 16, 1982, *Stutts 1207* (GA); Mun. Jaguariaiva, campo, February 5, 1910, *P. Dusen 9192* (BM, US); Mun. Laranjeiras do Sul, km 127, February 12, 1969, *Hatschbach 21142* (MBM); Mun. Ponta Grossa, Rio Barrozinha, BR 376, campo, March 6, 1982, *Stutts 1304* (GA); Mun. Ponta Grossa, Vila Velha, campo, February 11, 1968, *N. Imaguire 390* (CTES); Mun. Ponta Grossa, Rio Tibagi, campo, February 12, 1982, *Stutts 1178* (GA); Mun. Ipiranga, 23 km E of Imbituva, BR 373, km 29, campo, March 5, 1982, *Stutts 1286* (GA); Mun. Palmeira, Colonia Francese, BR 277, km 180, ca. 3 km E of Rio Capivara, campo, March 4, 1982, *Stutts 1279* (GA). SANTA CATARINA: Mun. Abelardo Luz, 7 km N of Abelardo Luz, campo, 5–600 m alt., February 19, 1957, *L. B. Smith & R. M. Klein 11477* (HBR, LP, R). **Paraguay:** Sierra de Amambay, in campis Ponta Pora, December, 1907, *Hassler 9892* (BM, G).

Vernonia series **Nudiflorae** S. Jones p.p. (emend. Stutts)

Vernonia series *Nudiflorae* S. Jones, Rhodora 81: 437. 1979. TYPE SPECIES: *Vernonia nudiflora* Less.

Fruticose or suffrutescent perennials with a xylopodium; stems one to several from the xylopodium, generally not branched below the inflorescence; inflorescences corymbose-paniculate; heads several to numerous, pedicellate, with 10–30 florets; involucre campanulate to approaching turbinate.

Vernonia subseries **Nudiflorae.** TYPE SPECIES: *Vernonia nudiflora* Less.

Fruticose or suffrutescent perennials with a xylopodium; leaves linear or linear-lanceolate; heads with 10–20 florets. Otherwise having the general characters of the series.

12. *Vernonia nudiflora* Less., Linnaea iv: 258. 1829. TYPE: BRAZIL: Brasilia meridionalis, *Sellow s.n.* (HOLOTYPE: not extant). LECTOTYPE here designated: (ISOTYPE at G-DC, as IDC michrofiche!).

Fruticose or suffrutescent perennial up to 1.5 m tall; stems ascending, upper portions with T-shaped or sericeous hairs. Leaves cauline, only slightly reduced upwards, sessile; blades linear, 4–8(10) cm long, 0.1–0.16(0.2) cm wide, length/width ratio ca. 40–60; punctate-glandular and becoming glabrous with age above; covered with T-shaped or sericeous hairs below; acute at the apex; more or less rounded at the base; margins entire and strongly revolute. Inflorescences corymbose-paniculate. Heads with 10(15)–20(25) florets, pedicellate; pedicels (5)8–30(35) mm long. Involucres more or less campanulate, (5)6–9(10) mm tall; phyllaries ca 20–25, imbricate in 4–5 series; inner phyllaries typically thinly glandular near the apex

and normally purple at the tip, pubescent near the margins or glabrous, 4.5–6.5 mm long, 1–1.7 mm wide, rounded to acute at the apex; outer phyllaries glabrous or pubescent near the margins, 0.8–1.4 mm long, 0.4–0.8 mm wide, acute at the apex. Corollas purple, the tube (4.5)5 6.5(8) mm long, the lobes (2.5)3.5–4.5(5.5) mm long, the tube ca. 1.5 times as long as the lobes. Anthers (2.7)3–4(4.5) mm long. Style branches (2)3–3.5(4) mm long. Pappus white to pale tan; inner series of 50–60 bristles (5)6–7 mm long; outer series 0.5–0.7 mm long. Achenes pubescent and glandular-dotted, (2.5)3–3.5 mm long, 0.8–1 mm wide, length/width ratio 3–4.

Vernonia nudiflora occurs in scattered areas of the campos of the southern Brazilian planalto, from Uruguay and northern Argentina north to Paraná, Brazil (Figure 8). Flowering occurs from December through April.

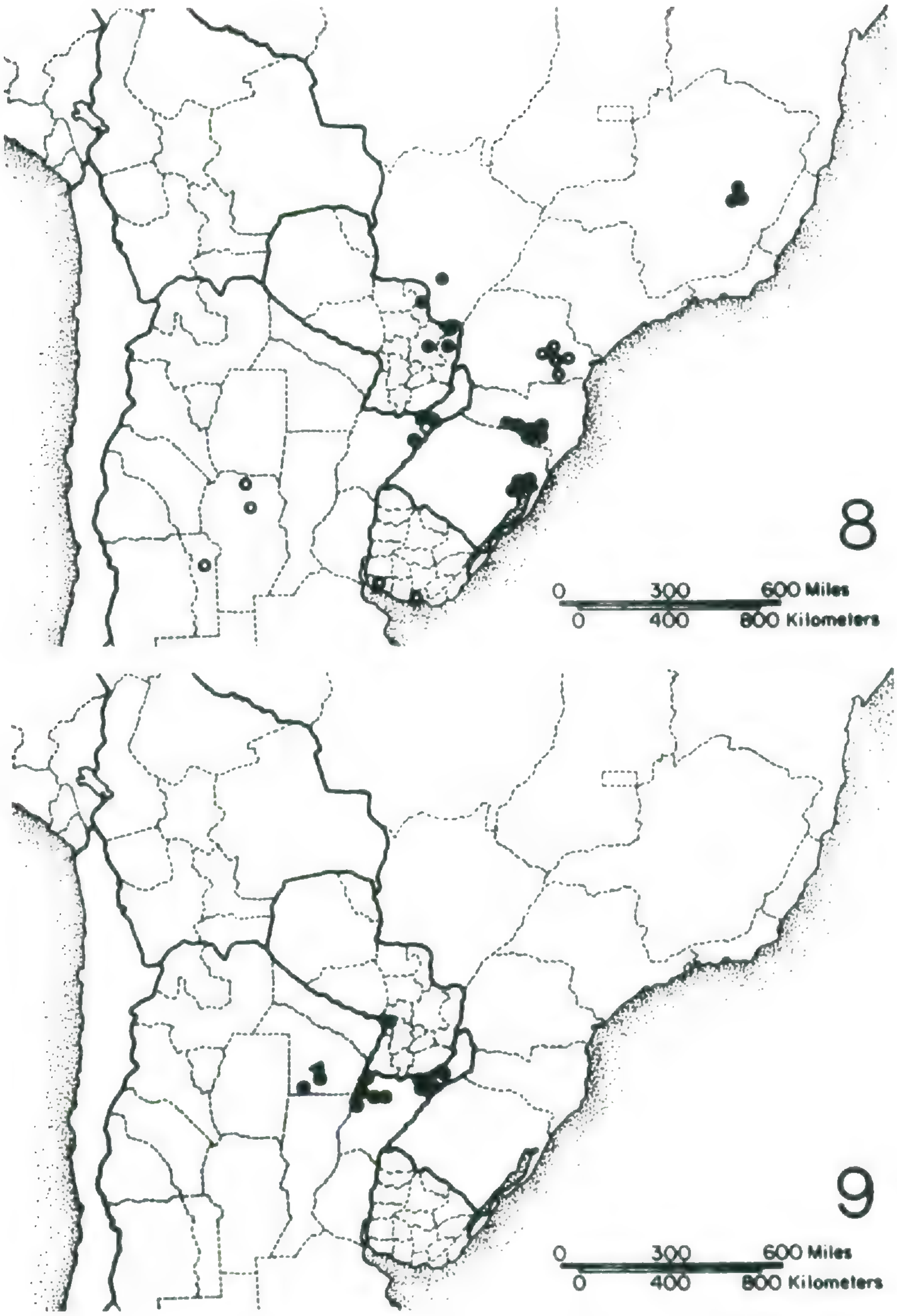
Vernonia nudiflora is easily distinguished from other species in the subsection by its narrowly linear leaves.

REPRESENTATIVE SPECIMENS: **Brazil:** PARANÁ: Mun. Ponta Grossa, BR 376, Rio Tibagi, campo, ca 800 m alt., February 12, 1982, *Stutts 1180* (GA); Mun. Ipiranga, BR 373, km 29, 23 km E of Imbituva, grazed campo, March 5, 1982, *Stutts 1287* (GA); Mun. Palmeira, BR 277, 2.7 km W of Rio Capivara, km 185, March 4, 1982, *Stutts 1283* (GA); Mun. Campo Largo, Rio Papagaio, campo, 930 m alt., February 23, 1950, *Hatschbach 6788* (RB); Mun. Porto Amazonas, 5 km N of Porto Amazonas, campo, February 6, 1981, *Hatschbach 43563* (GA, MBM). SANTA CATARINA: Mun. Lajes, estrada do Rodagem Federal, 3 km S of Lajes, campo, 900 m alt., February 12, 1957, *L. B. Smith & R. M Klein 11297* (HBR, LP); Mun. Lajes, 10 km E of Capão Alto, 900–1000 km alt., February 12, 1957, *L. B. Smith & R. M Klein 11340* (HBR, LP); Mun. Lajes, Passo do Socorro, campo, 800 m alt., April 13, 1982, *P. Reitz & R. M. Klein 14842* (HBR, LP). RIO GRANDE DO SUL: Mun. Guaiba, BR 116, km 32, Fazenda S. Maximiano, campo, February 17, 1976, *Matzenbacher 433* (GA). **Argentina:** PROV. CORDOBA: Depto. Rio Seco, Cerro Colorado, January 30, 1942, *Maldonado 1020* (LP); Depto. Calamuchita, 20 km NW of Santa Rosa de Calamuchita, environs of Ahos Pampa, 1000 m alt., January 26, 1974, *J. Conrad 2413* (GA, MO). PROV. SAN LUIS: Solosta, February, 1933, *Vignati 424* (LP). **Uruguay:** DEPTO. COLONIA: Punta Gorda, November 30, 1932, *Cabrera 2626* (SP). DEPTO. MONTEVIDEO: Jardem Botanico de Facultad de Agronomia de Montevideo, March 30, 1973, *Rosengurtt 11362* (GA, MVFA).

13. *Vernonia lucida* Less., Linnaea iv: 260. 829. TYPE: BRAZIL: Brasilia meridionalis misit *Sellow s.n.* (HOLOTYPE: not extant). LECTOTYPE here designated: (ISOTYPE at G-DC, as IDC microfiche!).

Cacalia lucida (Less.) Kuntze, Rev. Gen. Plant. 2: 970. 1891.

Vernonia nitidula Less. var. *lucida* (Less.) Arechavaleta, Anales Mus. Nac. Montevideo 3: 123. 1901.



Figures 8 and 9. Distribution of *Vernonia* subsect. *Chamaedrys* in southern South America. **8.** *V. nudiflora* (o) and *V. lucida* (●). **9.** *V. cupularis* (●), *V. chaquensis* (o) and *V. schulziana* (▲).

Suffrutescent perennial up to 1 m tall; stems more or less ascending, glabrous. Leaves cauline, somewhat reduced upwards, subcoriaceous, sessile; blades narrowly lanceolate, (3.5)5–10(14) cm long, 0.4–1.5 cm wide, length/width ratio (6)10(15); punctate-glandular above, occasionally scabrous; punctate-glandular below, the glands often dark in color; acute at the apex, often with a mucronate tip; varying from cuneate to rounded to truncate at the base; margins serrulate, subrevolute between teeth. Inflorescences corymbose-paniculate. Heads with (8)10–12(13) florets, pedicellate; pedicels (5)8–20(25) mm long. Involucres more or less campanulate with some tendency toward turbinate, (5)6–7(8.5) mm tall; phyllaries ca. 20, imbricate in 3–4 series; inner phyllaries glabrous and glandular near the apex, normally purple at the tip, (4.5)5.5–6.5(7) mm long, (1)1.3–1.7(1.9) mm wide, rounded to occasionally acute at the apex; outer phyllaries glabrous, often purple at the tip, (1)1.5–2(2.5) mm long, (0.6)0.8–1.2(1.6) mm wide, acute to obtuse at the apex. Corollas purple, fading with age, the tube (5)5.5–6(6.2) mm long, the lobes (2.5)3–4(4.7) mm long, the tube ca 1.5–2 times as long as the lobes. Anthers 3–4 mm long. Style branches (2.5)3(3.5) mm long. Pappus pale tan; inner series of 40–60(70) bristles (5)5.5(6) mm long; outer series (0.5)0.8–1.5(2) mm long. Achenes pubescent to thinly pubescent and thinly glandular-dotted, 2.5–3.5 mm long, 0.8–1 mm wide, length/width ratio 3–3.5.

Vernonia lucida has a discontinuous distribution in areas of rocky dry campo in southern Brazil, northeastern Argentina, eastern Paraguay and adjacent Mato Grosso do Sul, Brazil. It also occurs in the Serra do Espinhaco in Minas Gerais, Brazil (Figure 8). Flowering occurs from December through March.

In addition to confusion with *V. oligolepis*, *V. lucida* is also occasionally mistaken for *V. nitidula* from which it is easily distinguished by its unbranched or sparsely branched suffrutescent habit up to 1 m tall with a xylopodium, while *V. oligolepis* is a highly branched shrub up to 3 m tall without a xylopodium.

REPRESENTATIVE SPECIMENS: **Brazil:** MATO GROSSO DO SUL: Entre Duourados e Ponta Porã, campo limpo, February 5, 1952, *M. Kuhlmann s.n.* (SP). MINAS GERAIS: Serra do Cipó, 24–28 k N or Rio Cipó, campo rupestre, 3,500 ft alt., January 31, 1980, *King & Almeda 8382* (US); Serra do Cipó, km 135, ca. 150 km N of Belo Horizonte, 1250 m alt., campo and gallery margin, February 19, 1968, *H. S. Irwin et al 20508* (RB, S, US); Serra do Cipó, km 120, ca 145 km N or Belo Horizonte, 1300 m alt., February 15, 1968, *H. S. Irwin et al 20174* (US). SANTA CATARINA: Rio Capinzal, campo, 590 m alt., February 27, 1916, *P. Dusen 17825* (GH, S); Mun. Capinzal, 7 km SE of Capinzal, campo, 5–600 m alt., February 28, 1957, *L. B. Smith*

& *R. M. Klein 11937* (HBR, LP, RB, ÙS); Mun. Lajes, estrada de Rodagem Federal, 1 km S of Lajes, campo, 900 m alt., February 12, 1957, *L. B. Smith & R. M. Klein 11282* (HBR, LP, RB). RIO GRANDE DO SUL: Mun. Porto Alegre, Morro da Policia, April 4, 1949, *I. J. Cristovao s.n.* (GH, MO, SP); Mun. Porto Alegre, Morro da Policia, March 2, 1923, *Malme 1527* (S). **Paraguay:** DEPTO. AMAMBAY: Sierra de Amambay, 1907–08, *Hassler 10225* (BM, GH). DEPTO. ALTO PARANÁ: Sierra de Maracayú, Yerbales, near Igatimi, *Hassler 4778* (BM, K, UC); Alto Paraná, 1909–10, *K. Fiebrig 6112* (GH). DEPTO. CAAGUAZÚ: Caaguazú, February, 1905, *Hassler 9016* (BM, GH, MO, NY, S, UC). **Argentina:** PROV. MISIONES: Depto. Posadas, 1907–08, *E. Ekman 1216* (S); Depto. Candelaria, March, 1964, *R. M. Crovetto 9977* (CTES). PROV. CORRIENTES: Depto. Santo Tome, Ayo. Garabi, April 13, 1974, *A. Krapovickas et al 25250* (CTES).

Vernonia subseries **Chaquenses.** TYPE SPECIES: *Vernonia chaquensis* Cabrera.

Suffrutescent perennials with a xylopodium; leaves varying from linear to narrowly lanceolate to narrowly elliptic to oblanceolate; heads with 10–30 florets. Otherwise having the general characters of the series.

14. *Vernonia cupularis* Chodat, Bull. Herb. Boissier, Ser. 2, 2: 299. 1902. TYPE: PARAGUAY: In campo pr. Itacurubi, January, *Hassler 3756* (HOLOTYPE: G!; ISOTYPES: BM!, F!, G—as photo F!, GH!, NY!).

Vernonia cupularis Chodat var. *oligocephala* Chodat, Bull. Herb. Boissier, Ser 2, 2: 300. 1902. TYPE: PARAGUAY: Cordillera de Altos, in dumeto, February, 1899, *Hassler 6050* (HOLOTYPE: G!).

Suffrutescent perennial up to 1.5 m tall; stems ascending. Leaves cauline, reduced upwards, sessile; blades linear to rarely narrowly lanceolate, 5–10(11.5) cm long, 0.3–0.8(1) cm wide, length/width ratio (10)15–30; slightly scabrous and punctate-glandular above; white to tan tomentose below; acute at the apex; cuneate at the base; margins entire and strongly revolute. Inflorescences corymbose-paniculate. Heads with 20–30 florets, short pedicellate; pedicels (2)4–8(12) mm long. Involucres more or less campanulate with some tendency toward turbinate, 12–15 mm tall; phyllaries ca. 40, imbricate in 6–8 series; inner phyllaries glabrous, 8–9.5 mm long, 0.8–1.6 mm wide, acuminate to acute at the apex; outer phyllaries glabrous, 2.5–5 mm long, 0.4–1.1 mm wide, acuminate to long acuminate at the apex. Corollas rosy-purple, the tube (7)8–9.5 mm long, the lobes 4.5–6 mm long, the tube ca. 1.5–2 times as long as the lobes. Anthers (3.7)4–4.6 mm long. Style branches 3–4.5 mm long. Pappus pale tan to white; inner series of 50–60 bristles 8–9 mm long; outer series

(0.5)0.8–1.5 mm long. Achenes thinly pubescent and glandular-dotted, 3.5–4 mm long, 0.8–1.2 mm wide, length/width ratio ca. 3.5–4.

Vernonia cupularis has a restricted distribution on the campos and similar habitats of northeastern Argentina and Paraguay (Figure 9). It has been collected from both dry and moist sites. Flowering occurs from January through March.

Vernonia cupularis is most easily confused with *V. schulziana,* a very rare species, from which it may be distinguished by its larger heads with more numerous florets and its larger achenes (involucres 12–15 mm tall vs. 8 mm tall; 20–30 florets vs. 18–20 florets per head; achenes 3.5–4 mm long vs. 2–3 mm long).

REPRESENTATIVE SPECIMENS: **Paraguay:** DEPTO. LA CORDILLERA: In regione lacus Ypacaray, Bernardino, January, *Hassler 11481* (G). **Argentina:** PROV. CORRIENTES: Depto. Mburucuyá, Estancia Santa Teresa, dry, sunny grassland on both clay and sandy soil, March 3, 1954, *T. M. Pedersen 2625* (BR, G, GH, S). PROV. MISIONES: Depto. San Ignacio, Foudo de Roas, 260 m alt., campo matorral, March 9, 1958, *Montes s.n.* (NY); Depto. Candelaria, Loreto, March, 1964, *R. M. Crovetto 9919* (CTES); Loreto, 218 m alt., February 13, 1945, *Montes 500* (S); Santa Ana, January 17, 1913, *Rodrigues 173* (GH); Santa Ana, March 27, 1946, *Montes 1998* (S).

15. *Vernonia chaquensis* Cabrera, Darwiniana 6: 358–360. 1944. TYPE: ARGENTINA: PROV. CHACO, Colonia Benitez, February, 1930, *A. G. Schulz 13* (HOLOTYPE: LP; ISOTYPE: CTES!).

Suffrutescent perennial up to 1 m tall; stems ascending, upper portions tomentulose. Leaves cauline, reduced upwards, sessile; blades narrowly elliptic to oblanceolate, 5.5–9 cm long, 1–2 cm wide, length/width ratio 3.5–4.5; thinly tomentose but tending to become more or less glabrous with age and punctate-glandular above, grey tomentose below, acute or occasionally acuminate at the apex; cuneate to attenuate at the base; margins serrate or serrulate to occasionally entire (the smaller upper leaves tending to have more or less entire margins), slightly revolute. Inflorescences corymbose-paniculate. Heads with (12)15 16 florets, short pedicellate to sessile; pedicels 1–4(8) mm long. Involucres more or less campanulate with some tendency towards turbinate, 6 8 mm tall; phyllaries ca. 30, imbricate in ca. 5 series; inner phyllaries tomentose and glandular near the apex, often purple, 4.5–6 mm long, (0.6)0.8–1.2 mm wide, acute to occasionally acuminate at the apex, occasionally with a very short mucro; outer phyllaries tomentose

and glandular near the apex, often thinly pubescent along the margins, 1.3–1.7 mm long, 0.6–0.8 mm wide, acute at the apex, occasionally with a very short mucro. Corollas purple, the tube 4.5–5.5 mm long, the lobes 3 -3.5 mm long, the tube ca. 1.5 times as long as the lobes. Anthers 3.3–3.8 mm long. Style branches ca. 2.5 mm long. Pappus white to pale tan; inner series of ca. 60 bristles 6–7 mm long; outer series (0.3)0.4–0.8(1.1) mm long. Achenes thinly pubescent and glandular-dotted, 2.5–3.5 mm long, 0.6–0.9 mm wide, length/width ratio 3–4.

Vernonia chaquensis is known only from the provinces of Corrientes and Chaco, Argentina where it occurs mostly in moist grasslands and roadsides (Figure 9). Flowering occurs in January and February, and sporadically later.

Vernonia chaquensis may be confused with *V. cupularis* from which it may be distinguished by having fewer florets per head, smaller heads and shorter inner pappus ((12)15–16 florets vs. 20–30 florets; involucres 6–8 mm tall vs. 12–15 mm tall; inner pappus 6–7 mm long vs. 8–9 mm long).

REPRESENTATIVE SPECIMENS: **Argentina:** PROV. CHACO: Villa Angela, campo alto, February 24, 1964, *A. G. Schulz 13683* (CTES); Santa Sylvina, Ruta 95, Estancia La Lonja, campo alto, humedo, February 25, 1964, *A. G. Schulz 13696* (CTES). PROV. CORRIENTES: Depto. Capital, Ruta 12, 20 km NE de Corrientes, Granja Yatay, January 22, 1976, *A. Schinini 12492* (CTES, G); Depto. Empedrado, Estancia La Yela, rough grassland on low wet ground, clay soil, January 25, 1966, *T. M. Pedersen 7717* (GH, RB, UC, US); Depto. Mburucuyá, Estancia Santa Maria, rough pastures on loamy soil, May 4, 1952, *T. M. Pedersen 1708* (BR, G, GH); Depto. Bella Vista, Raices, Colonia "3 de April", January 27, 1956, *T. M. Pedersen 3699* (BR, G, GH, MO, NY).

16. *Vernonia schulziana* Cabrera, Darwiniana 6: 361–363. 1944. TYPE: ARGENTINA: PROV. CHACO, Colonia Benitez, January, 1943, *A. G. Schulz 3757* (HOLOTYPE: SI; ISOTYPE: CTES!).

Suffrutescent perennial up to 1 m tall; stems ascending, upper portions tomentulose. Leaves cauline, reduced upwards, sessile; blades narrowly lanceolate, 8–12 cm long, 1–2.5 cm wide, length/width ratio 5–10; scabrous above, tomentulose below, acute at the apex; rounded at the base; margins serrulate to entire, slightly revolute. Inflorescences corymobose-paniculate. Heads with 18–20 florets, short pedicellate; pedicels up to 5 mm long. Involucres more or less campanulate with some tendency towards turbinate, ca. 8 mm tall; phyllaries ca. 30, imbricate in 4–6 series; inner phyllaries glabrous, 6–7 mm long, 1–1.5 mm wide, obtuse at the apex; outer

phyllaries glabrous, 2–3 mm long, ca. 1 mm wide, obtuse to acute at the apex. Corollas purple, the tube ca. 5 mm long, the lobes ca. 4 mm long, the tube ca. 1.25 times as long as the lobes. Anthers 3.7–4 mm long. Style branches 2.5–2.8 mm long. Pappus white to pale tan; inner series of ca. 35–40 bristles 5.5–7 mm long; outer series 0.6–1.2 mm long. Achenes pubescent and glandular-dotted, 2–3 mm long, ca. 0.8 mm wide, length/width ratio ca. 3.

Vernonia schulziana is known only from a few collections made near the type locality in the 1930's and 40's (Figure 9), and may not be extant. Flowering occurred in January for those collections seen.

REPRESENTATIVE SPECIMENS: **Argentina:** PROV. CHACO: Colonia Benitez, January, 1936, *A. G. Schulz 921* (CTES).

ACKNOWLEDGMENTS

I thank the curators of the following herbaria for the loan of specimens: A, BM, BR, CTES, E, F, G, G-DC, G-DEL, GH, K, LP, M, MBM, MO, NY, R, RB, S, SP, UC, and US.

I especially thank the Brazilian government for providing the necessary collecting permits. The following individuals were extremely kind and helpful during the time spent in Brazil: Dr. Gert Hatschbach and Dr. Ronaldo Kummrow of the Museu Botanico Municipal, Curitiba, Dr. Elsie F. Guimaraes, Dr. Graziela M. Barroso, Dr. Valério F. Ferreira and Dr. Gustavo Martinelli of the Jardim Botânico do Rio de Janeiro, Rio de Janeiro, and Dr. Pedro P. Carauta and Dr. Maria Célia Vianna of Herbário Alberto Castellanos, Instituto de Conservacão da Natureza, Rio de Janeiro.

The assistance of Dr. David Giannasi, Ms. Nancy Coile, Mr. Andy Tull, Dr. Gerald Smith, Dr. Jim Manhart, Mrs. Lynn Hill and Mrs. Anna Baker is gratefully acknowledged. Very special thanks are due to my wife, Robin, for her patience and understanding.

I am appreciative of the guidance and encouragement provided by my major professor Dr. Samuel B. Jones, Jr. during the course of this study, and for his and Nancy Coile's assistance in revising this manuscript.

LITERATURE CITED

BAKER, J. G. 1873. Compositae. I. Vernonieae. *In:* K. F. P. von Martius, Ed., Flora Brasiliensis 6(2): 6–179.

BENTHAM, G. AND J. D. HOOKER. 1873. Vernonieae. Genera Plantarum 2: 227–231.

CABRERA, A. L. 1944. Vernonieas Argentinas (Compositae). Darwiniana 6: 265–379.

_____ AND R. M. KLEIN. 1980. Compositae: Tribe Vernonieae. *In:* P. Reitz, Ed., Flora Ilustrada Catarinense, Part I. No. 3: 226–408, Herbário "Barbosa Rodrigues," Itajai, Santa Catarina, Brazil.

CANDOLLE, A. C. P. de. 1914. Trois Monstruosités Végétales. Bull. Soc. Bot. Genève, Ser. II, 7: 228–231.

CANDOLLE, A. P. de. 1836. Prodromus 5: 15–16, 48.

CASSINI, H. 1817. Apercu des genres nouveaux formés par M. Henri Cassini dans la famille des Synanthérées. Bull. Scient. Soc. Phil. 4: 66.

_____. 1819. Sur la famille des Synanthérées contenant les caractéres des tribus. J. Phys. Chim. Hist. Nat. Arts. 88: 190–204 (cf. pp. 203–204).

CHAPMAN, G. C. AND S. B. JONES, JR. 1971. Hybridization between *Senecio smallii* and *S. tomentosus* (Compositae) on the granite flatrocks of the southeastern United States. Brittonia 23: 209–216.

CHODAT, R. 1902. Plantae Hasslerianae. Bull. Herb. Boissier Ser. 2, 2: 409.

COVAS, G. AND J. H. HUNZIKER. 1954. Estudios Cariologicos en Antofitas. IV. Parte. Inagro 8(3): 249–253.

CRAWFORD, D. J. AND F. G. HAWKSWORTH. 1979. Flavonoid chemistry of *Arceuthobium* (Viscaceae). Brittonia 31: 212–216.

CUATRECASAS, J. 1965. Some new compositae from Peru. Ann. Missouri Bot. Gard. 52: 304–313.

EITEN, G. 1972. The Cerrado Vegetation of Brazil. The Botanical Review 38(2): 201–341 (cf. pp. 204).

EKMAN, E. L. 1914. West Indian Vernonieae. Ark. Bot. 13(15): 1–106.

ERDTMAN, G. 1966. Pollen Morphology and Plant Taxonomy. Angiosperms. Hafner Pub. Co., N.Y.

GIANNASI, D. E. 1975. The flavonoid systematics of the genus *Dahlia* (Compositae). Mem. New York Bot. Gard. 26(2): 1–125.

GLEASON, H. A. 1906. A revision of the North American Vernonieae. Bull. New York Bot. Gard. 4: 144–243.

_____. 1922. Vernonieae. N. Am. Flora 33: 52–95.

HARBORNE, J. B. AND C. A. WILLIAMS. 1977. Vernonieae: Chemical Review. *In:* Heywood, V. H., et al. The Biology and Chemistry of the Compositae. Vol. I. Academic Press, N.Y.

HUNTER, G. E. 1964. Chromosome numbers in *Vernonia:* section *Lepidoploa* subsection *Paniculatae verae*. Southw. Naturalist 9(4): 239–244.

JONES, S. B., JR. 1970. Scanning electron microscopy of pollen as an aid to the systematics of *Vernonia*. Bull. Torrey Bot. Club. 97: 325–335.

_____. 1974. Vernonieae (Compositae) chromosome numbers. Bull. Torrey Bot. Club 101: 31–34.

_____. 1976. Revision of *Vernonia* (Compositae) subsection *Paniculatae* series *Umbelliformes* of the Mexican highlands. Rhodora 78: 180–206.

_____. 1979a. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the New World. Rhodora 81: 425–447.

_____. 1979b. Chromosome numbers of Vernonieae (Compositae). Bull. Torrey Bot. Club 106: 79–84.

_____. 1981a. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the Old World. Rhodora 83: 59–75.

_____. 1981b. Revision of *Vernonia* series *Flexuosae* (Compositae: Vernonieae). Brittonia 33(2): 214–224.

———. 1982. A Revision of *Vernonia* series *Buddleiifoliae* (Compositae: Vernonieae). Brittonia 34(1): 102–117.

———, W. Z. Faust and L. E. Urbatsch. 1970. Natural hybridization between *Vernonia crinita* and *V. baldwini* (Compositae). Castanea 35: 61–67.

Keeley, S. C. and S. B. Jones, Jr. 1979. Distributions of pollen types in *Vernonia* (Vernonieae: Compositae). Syst. Bot. 4(3): 195–202.

Lessing, C. F. 1829. De synanthereis Herbarii regii berolinensis dissertationes, I. Vernonieae. Linnaea iv: 240–356.

———. 1831a. De Synanthereis dissertatio quarta. Linnaea vi: 240–288; 295–339.

———. 1831b. De Synanthereis Herbarii regii berolinensis dissertationes, IV. Vernoniearum mantissa. Linnaea vi: 624–721.

Mabry, T. J., Z. Abdel-Baset, W. G. Padolina and S. B. Jones, Jr. 1975. Systematic implications of flavonoids and sesquiterpene lactones in species of *Vernonia*. Biochem. Syst. and Ecol. 2: 185–192.

Malme, G. O. 1933. Compositae Paranense Dusenianae. Kongl. Svenska Vetenskapsakad. Handl. Band 12, 2: 22–24.

Miller, G. J. 1977. The origin of a hybrid *Vernonia* colony on Pine Mt., Georgia. Castanea 42: 31–38.

Picman, A. K., P. C. Ranieri, G. H. N. Towers and J. Lam. 1980. Visualization reagents for sesquiterpene lactones and polyacetylenes on thin layer chromatograms. J. Chromatography 189: 187–198.

Radford, A. E., W. C. Dickison, J. R. Massey, C. R. Bell. 1974. Vascular Plant Systematics. Harper and Row, N.Y.

Schultz-Bipontinus, C. H. 1861. Cassiniaceae uniflorae, oder Verzeichniss der Cassiniaceen mit 1-bluthigen kopfchen. Jahresber. Pollichia 18/19: 157–190.

———. 1863. *Lychnophora* Martius und einige benachbarte Gattungen. Jahresber. Pollichia 20/21: 321–439.

Smith, C. E., Jr. 1971. Observations on stengelioid species of *Vernonia*. Agricultural Handbook No. 396, USDA, U.S. Government Printing Office, Washington, D.C.

Steyermark, C. S. 1939. Distribution and hybridization of *Vernonia* in Missouri. Bot. Gaz. 100: 558–562.

Stutts, John G. 1981. Taxonomic revision of *Pollalesta* H.B.K. (Compositae: Vernonieae). Rhodora 83: 385–419.

———. 1983. A new name in *Vernonia* (Compositae). Brittonia 35(4): 351–352.

Yoshioka, H., T. J. Mabry and B. Timmermann. 1973. Sesquiterpene Lactones. Univ. of Tokyo Press.

BOTANY DEPARTMENT
UNIVERSITY OF GEORGIA
ATHENS, GA 30602

NEW ENGLAND NOTE

CALOPOGON TUBEROSUS VAR. *LATIFOLIUS* (ST. JOHN) BOIVIN (ORCHIDACEAE) NEW TO THE UNITED STATES

Great Wass Island, with its significant geological features of deep, cold, tidal pools, steep red-granite ledges and raised peatlands, has become a mecca for botanists over the past twenty years. Its characteristic boreal flora includes: *Iris hookerii* Penny, *Sedum rosea* (L.) Scop., *Primula laurentiana* Fern., *Montia lamprosperma* Cham., *Lomatogonium rotatum* (L.) Fries, and *Mertensia maritima* (L.) Gray. The presence of these plants was one reason for The Nature Conservancy acquiring most of the island nine years ago. Located in Maine's most easterly county—Washington, the island lies one mile south of Jonesport in the Gulf of Maine.

During the summer of 1982, Dr. George Newman and I were exploring a raised peatland in the center of the island which is known locally as Baked Appleberry Bog. In the bog among the stunted *Pinus banksiana* Lamb., *Rubus chameamorus* L., and *Empetrum nigrum* L., were quantities of a small single broad-leaved orchid which we assumed was *Arethusa bulbosa* L. After having up-rooted two specimens and noting the large corms, we felt our identification was correct. In lieu of returning the plants to their original habitat we planted them in an artificial setting at home for further study. In late June of the following season, the plants produced flowers showing them to be *Calopogon tuberosus* var. *latifolius* which is new to the United States. It is not surprising that this variety should occur at Great Wass; Roland and Smith (1969) record it from Nova Scotia and Magdalen Islands.

On July 4, 1983 Carlton Crowley and I revisited Great Wass to photograph and collect flowering material. Specimens were deposited in NEBC and MEO herbaria.

LITERATURE CITED

ROLAND, A. E. AND E. C. SMITH. 1969. The Flora of Nova Scotia. Nova Scotia Museum.

L. M. EASTMAN
R.R. 2 BOX 3040
GREENE, MAINE 04236

THE 1987 JESSE M. GREENMAN AWARD

The 1987 Jesse M. Greenman Award has been won by Geoffrey A. Levin for his publications "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus," "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic Analysis," which appeared in the Annals of the Missouri Botanical Garden, volume 73, number 1, and "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic Analysis," which was published in Systematic Botany, volume 11, number 4. This series of papers is derived from a Ph.D. dissertation from the University of California, Davis, under the direction of Drs. James A. Doyle, Grady L. Webster, and Jack A. Wolfe. Dr. Levin uses a large set of characters (in this case leaf characters) to address questions of systematic relationships and phylogeny at higher taxonomic levels, using the results from both phenetic and cladistic analysis to evaluate a more traditional classification system, and to identify genera or groups of genera whose position and relationship are not clear and therefore are in need of additional study.

The Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the previous year. Papers published during 1987 are now being considered for the 20th annual award, which will be presented in the summer of 1988. Reprints of such papers should be sent to:

Greenman Award Committee
Division of Research
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1988 award, reprints must be received by 1 June 1988.

NEBC SYMPOSIUM

The New England Botanical Club is planning a regional symposium entitled "Plant Conservation: A Biogeographical Perspective." This symposium will be held at Harvard University in Cambridge, Massachusetts on Friday evening and all day Saturday, 6 7 May, 1988.

The aim of the symposium will be to address plant conservation in a biogeographic framework. There will be keynote speakers on Friday evening and Saturday morning, followed by three paper sessions on Saturday on the following topics:

Biogeographical Perspectives
New England States Plant Conservation
Research on New England Taxa

Proceedings will be published in a regular issue of RHODORA. For further information, please contact:

Symposium
New England Botanical Club
Harvard University Herbaria
22 Divinity Avenue
Cambridge, MA 02138

ACQUISITION POLICY OF THE NEW ENGLAND BOTANICAL CLUB VASCULAR PLANT HERBARIUM (NEBC)

INTRODUCTION

This statement of policy has been prepared to provide information about the New England Botanical Club Vascular Plant Herbarium (NEBC), to make known the need for improvement of the collections and to outline various ways in which collectors may contribute to this end. By specifying minimum standards for specimens and the nature of the decisions that will be made in accepting specimens, it is hoped that interested parties will collect or photograph specimens for the NEBC Herbarium from an informed perspective.

The NEBC Herbarium comprises nearly a quarter of a million specimens and is without question the most extensive collection of plants from the New England region. In spite of the admirable efforts of past botanists, both amateur and professional, there is considerable room for improvement of the collections. Club members and others can play a significant role in the upgrading of the Herbarium to make it of more value to the varied research and reference interests that it serves.

OBJECTIVES

One primary objective of the herbarium is to represent the diversity of plants, both indigenous and introduced, that have occurred and do occur spontaneously in New England. Virtually all species of native New England plants are already represented in the collection, although coverage is a little less complete for the infraspecific taxa reported to occur in the region. Adventive species will undoubtedly make up the majority of new taxa added to the Herbarium.

A second important objective is to represent the widest geographical range attained by each taxon in New England. It is impossible for the herbarium to attempt to verify the present day occurrence of each taxon, but for certain plants known to be rare within a state the addition of a recent collection to substantiate an old record would be an acceptable exception. Information about the spread or disappearance of species may often be derived from the collection, but it is not an objective to document such changes.

Regular patrons of the Herbarium may have noticed that certain

regions of New England tend to be poorly represented, while others tend to be particularly well represented in the collections. The metropolitan Boston area and Coos County, New Hampshire, are examples of the latter. Some under-represented areas are: Piscataquis, Somerset and Waldo counties, Maine; Belknap, Merrimack and Sullivan counties, New Hampshire; Caledonia, Franklin, Lamoille, Orange and Washington counties, Vermont; Hampden and Hampshire counties, Massachusetts; Bristol, Kent and Newport counties, Rhode Island; and Tolland and Middlesex counties, Connecticut. Collectors who provide specimens from poorly collected areas will help to give a much needed geographical balance to the herbarium.

Taxonomically difficult genera (such as *Crataegus* and *Isoetes*) tend to be under-collected. Many species known to be widely distributed and common in occurrence are unevenly or poorly represented *because* they are so common. Some plants are preferentially collected over others (for example *Trillium* over *Taraxacum*) giving a distorted picture of their actual distribution and frequency of occurrence in nature. Patrons of the Herbarium should note such instances and draw them to the attention of the curators.

In addition to information about species diversity and geographical distribution, herbarium specimens provide phenological, ecological and taxonomic data for floristic, systematic and ecological studies. Opportunities exist to improve substantially data on many of the older collections. Collectors in the past rarely provided detailed locality and habitat data or field observations (size, habit of growth, colors, odors, and details of other characteristics not obvious from the dried specimen). Sequential collecting from tagged plants was and is rarely done. A novice can provide a specimen of exceptional quality merely by taking a little more care in collecting. Certain features of plants are rarely found in collections. Winter buds of woody plants and winter forms of some herbs are examples. For positive identification such specimens should be accompanied by material of the same plant (woody) or station (herbaceous) collected in flowering or fruiting condition. Ideally, a specimen of a woody plant would include flowers, fruits, foliage and winter buds from the same tagged plant. Fern specimens should include both fertile and sterile fronds with the underground parts (and gametophytes if feasible!). Specimens of herbaceous plants should include the underground parts and have flowers or fruit, or both.

MINIMUM STANDARDS

Specimens added to the NEBC Herbarium comprise pressed plants, photographs or photocopies of pressed plants, or photographs of plants in nature. More than one photograph of a plant may be needed for accurate identification.

All specimens must meet the following requirements before they can be considered for addition to the NEBC Herbarium:

1) The specimen must have been collected or photographed in New England (Maine, New Hampshire, Vermont, Massachusets, Rhode Island, Connecticut). Locality must be provided at least to town level, and preferably more exactly.
2) The specimen must bear flowers or fruit (vegetative specimens of taxa where mature foliage is not available at the time of flowering or fruiting (Lemnaceae, *Salix, Populus, Ulmus, Acer,* etc.) are acceptable, but attempts to correlate sterile specimens of these plants with fertile material from the same individual is encouraged). Specimens must be collected at the proper stage for accurate identification. For example, flowering or sterile specimens of *Quercus* are of limited or no value, ideal specimens should include mature acorns; collections of Apiaceae should include mature fruit.
3) The collection or photograph must represent the spontaneous occurrence of the plant growing outside of cultivation.
4) The label data must include the name(s) of the collector and date of collection. Collection numbers, used by nearly all professional botanists, are convenient in citing exact specimens in monographic, revisionary and other kinds of studies.
5) The specimen must be a collection of the actual plant unless (for rare taxa) such collection would endanger the population. Photographic documentation would then be acceptable.

The following additional types of information are strongly recommended:

1) The label should bear ecological information that would help an investigator recreate an accurate picture of the habitat. Population size, elevation, soil type, slope, exposure, dominant trees and associated plants are highly desirable data.
2) The label should bear information (growth habit, colors, odors, surface textures, height and dbh of trees, etc.) about the

living plant that will not be evident in the dried specimen. For example, virtually all specimens of *Quercus palustris* Muenchh. fail to mention the drooping lower branches and relatively unforked bole, characteristics that in life allow for quick identification.

3) Except for standard abbreviations for units of measure (mm, cm, km, etc.), compass directions (N, E, S, W), or for the words 'about' or 'approximately' (ca.) the use of abbreviations on herbarium labels should be avoided.
4) A scale to show the dimensions of a plant should be provided in photographs.

GENERAL ACQUISITION POLICY

While the NEBC Herbarium is eager to accept type specimens, new state or county records, collections of rare and endangered plants from new stations, and specimens specifically cited in scientific publications, the majority of specimens will not fall into these categories. Fulfilling the objectives outlined above will require the addition of a significant amount of new material. To avoid an unreasonable demand for more cabinet space the herbarium staff will seek to use efficiently all space currently available by eliminating pointless duplication in current holdings and exercising judgment in accepting new material.

It is not desirable to accept every township record for common or abundantly occurring taxa. Only a sufficient number of specimens to establish the frequency and extent of occurrence is required. Some duplicate records of common species may be retained for reasons of historical interest, or because they exhibit features rarely found in herbarium specimens. For example, a specimen with staminate catkins of *Salix sericea* Marshall, a species common in many areas would be retained or added to the collection regardless of prior collection from the same township since plants of this species with staminate inflorescences are infrequent.

The Herbarium staff will attempt to insure that material added to the collection is adequate for defining geographic distribution and in providing quality research material for monographers, biosystematists and others with a need for well preserved, accurately labeled specimens. Specimens meeting minimum standards, but which are not added to the NEBC Herbarium will be made available to other herbaria with an interest in the New England flora. Such specimens will not only be of scientific value at other institutions,

but can help improve the NEBC Herbarium by virtue of the material that may be received in exchange. Specimens failing to meet minimum standards for scientific usefulness will be returned to the collector or discarded.

Botanists interested in the flora of New England are encouraged to assist in the improvement of the NEBC Herbarium and should not hesitate to consult with the curators about suggested improvements in order to contribute most efficiently and effectively to this valuable resource.

NEBC Vascular Plant Herbarium Committee
Ray Angelo, Chairman

BOOKS RECEIVED

DELCOURT, PAUL A., HAZEL R. DELCOURT AND THOMPSON WEBB III. *Atlas of Mapped Distributions of Dominance and Modern Pollen Percentages for Important Tree Taxa of Eastern North America.* 133 pp. American Association of Stratigraphic Palynologists Foundation, Contribution Series no. 14, April 1984. ISSN 0160-8843. (P.O. Box 819047, Dallas TX 73581, $9.00)

This atlas summarizes "the contemporary distributions of major tree taxa and their corresponding pollen percentages across eastern North America." The authors present paired maps: contoured isophyte maps of percent value of growing stock volume (GSV) and isopoll maps of arboreal pollen percentages (AP), for 24 major tree taxa (*Abies, Acer, Betula, Carya,* etc.) plus GSV maps for 8 more taxa. Scatter plots of %GSV and %AP illustrate the relationships of dominance in the vegetation to pollen production and dispersal for 20 important tree taxa. These data were also subjected to geometric-mean linear regression analysis. There follows a discussion of the map patterns and pollen-vegetation relationships of the various taxa. These data should "provide the foundation for the use of modern analog and taxon calibration approaches for quantification of late Quaternary vegetational history in eastern North America."

FLEURBEC. (LAMOUREAUX, GISELE, ED.). *Plantes Sauvages du Bord de la Mer.* 286 pp. 1985. Fleurbec, 415 A. Chemin du Roy, Saint-Augustin, Québec, Canada G0A 3E0 (or order from Ministère des Communications, Direction de la Commercialisation, C.P. 1005, Québec Canada, G1K 7B5, $9.95 Canadian.)

This book is the latest in a series of attractive useful French language guides for the layman to the native plants of Québec. It treats seashore plants beginning with a good introduction to seashore ecology. The 56 representative plants are grouped by flower color, those resembling grasses, shrubs, algae. The detailed description of each includes a range map of Canadian, and sometimes U.S., distribution, excellent close-up and good habitat photographs, technical details, uses, history, etc. There is an excellent 9-page bibliography.

"Fleurbec" is a group of Québec botanists and collaborators dedicated to producing this series of books to spread knowledge of their

common plants to the people of Québec. An index to plants treated in earlier books is included. Titles are *Plantes Sauvages Comestibles, Plantes Sauvages Printanières, Plantes Sauvages des Villes et des Champs, Vol. 1,* and *Plantes Sauvages des Villes, des Champs, et en Bordure des Chemins, Vol. 2.*

IRELAND, ROBERT R. AND LINDA M. LEY. *Type Specimens of Bryophytes in the National Museum of Natural Sciences, National Museums of Canada.* Syllogus No. 47, 69 pp., 1984. (Available from National Museums of Canada, National Museum of Natural Sciences, Ottawa, Ontario, Canada K1A 0M8.)

This publication is a catalogue of 848 moss and 86 liverwort taxa. The authority, literature citation, kind of type, locality information, collection number or date, CANM accession number, and current accepted name are given for each taxon. The historical Macoun herbarium specimens are listed separately.

MARY M. WALKER
NEBC LIBRARY COMMITTEE

Vol. 89, No. 860, including pages 347–460, was issued October 30, 1987

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8") **throughout** including tables, figure legends, and literature citations. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

RHODORA January 1988 Vol. 90, No. 861

CONTENTS

Regrowth of a decimated population of Panax quinquefolium in a Missouri climax forest
Walter H. Lewis 1

Papaver L. sect. Californicum Kadereit, a new section of the genus
Joachim W. Kadereit 7

The taxonomic status of Potamogeton lateralis Morong (Potamogetonaceae)
C. Barre Hellquist, C. Thomas Philbrick and *Robert L. Hilton* . . 15

A floristic inventory of the Gateway National Recreation Area, New York–New Jersey
Richard Stalter and *Andrew Greller* 21

Ranunculus ×spitzbergensis (Nath.) Hadač, an addition to the flora of North America
William J. Cody, Marcel Blondeau and *Jacques Cayouette* . . . 27

Taxonomic revision of Vernonia subsect. Chamaedrys (Compositae: Vernonieae)
John G. Stutts 37

NEW ENGLAND NOTE

Calopogon tuberosus var. latifolius (St. John) Boivin (Orchidaceae) new to the United States
Leslie Eastman 101

ANNOUNCEMENTS

Jesse M. Greenman Award 103
NEBC Symposium 104
NEBC Herbarium Acquisition Policy 105
Books Received 111
Instructions to Contributors . . . . . inside back cover

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 90 April 1988 No. 862

The New England Botanical Club, Inc.

22 Divinity Avenue, Cambridge, Massachusetts 02138

RHODORA

NORTON H. NICKERSON, Editor-in-Chief

Associate Editors

DAVID S. BARRINGTON
A. LINN BOGLE
DAVID E. BOUFFORD
WILLIAM D. COUNTRYMAN
GARRETT E. CROW
RICHARD A. FRALICK
GERALD J. GASTONY
C. BARRE HELLQUIST
MICHAEL W. LEFOR
ROBERT T. WILCE

ISSN 0035-4902

RHODORA.—Published four times a year, in January, April, July, and October by the New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138. Second Class postage paid at Boston, MA. A journal of botany devoted primarily to the flora of North America. Price $25.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to 22 Divinity Avenue, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related areas, and articles concerned with systematic botany and cytotaxonomy in their broader implications will be considered. Brevity is urged; please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Fifty reprints of each article are supplied free of charge. Authors may arrange with Lexington Press for additional copies. RHODORA assesses page charges.

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

POSTMASTER: Send address changes to RHODORA, 22 Divinity Avenue, Cambridge, MA 02138.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS 02173

Cover Illustration

Eupatorium leucolepis var. *novaeangliae* is an endemic New England taxon restricted to upper margins of sandy-peaty coastal plain ponds. Currently vouchered from 7 ponds in MA and 5 in RI (several historical stations are extirpated), New England Boneset is a candidate for federal listing. The nominate variety occurs from Long Island in NY (very rare) and southern NJ to FL and LA.

Original artwork by Caren Caljouw

Rhodora

(ISSN 0035 4902)

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 90 April 1988 No. 862

A SURVEY OF FLORAL VARIATION IN FIVE POPULATIONS OF *PODOSTEMUM CERATOPHYLLUM* MICHX. (PODOSTEMACEAE)[1]

C. Thomas Philbrick[2] and A. Linn Bogle

ABSTRACT

Previously undescribed variation in the floral morphology of *Podostemum ceratophyllum* Michx. is reported. The numbers of tepals and anthers per flower are shown to differ widely among five selected populations in the northeastern United States. Per flower variation in tepal number ranges from one to seven, and of anthers from two (typical) to seven. Genetic rather than environmental factors are postulated to be responsible for this variation. Vegetative reproduction and the autogamous breeding system may be important factors in maintaining floral polymorphism.

Key Words: *Podostemum ceratophyllum*, floral morphology, northeastern United States

INTRODUCTION

The Podostemaceae (Riverweeds), a family of about 45 genera of moss- or alga-like aquatic flowering plants, are largely restricted to swiftly flowing streams, rapids and waterfalls of the tropics and subtropics (Graham & Wood, 1975). The thalloid plants apparently lack roots, their prostrate stems attaching to the surfaces of submerged rocks by means of adhesive-secreting, holdfast-like organs termed "haptera" (Graham & Wood, 1975; Philbrick, 1984). Members of the family have long been recognized as highly unusual and fascinating due to their bizarre morphology, anatomy, reproductive systems and ecology; yet, for the great majority of taxa, only

[1]Scientific Contribution Number 1536 from the New Hampshire Agricultural Experiment Station.

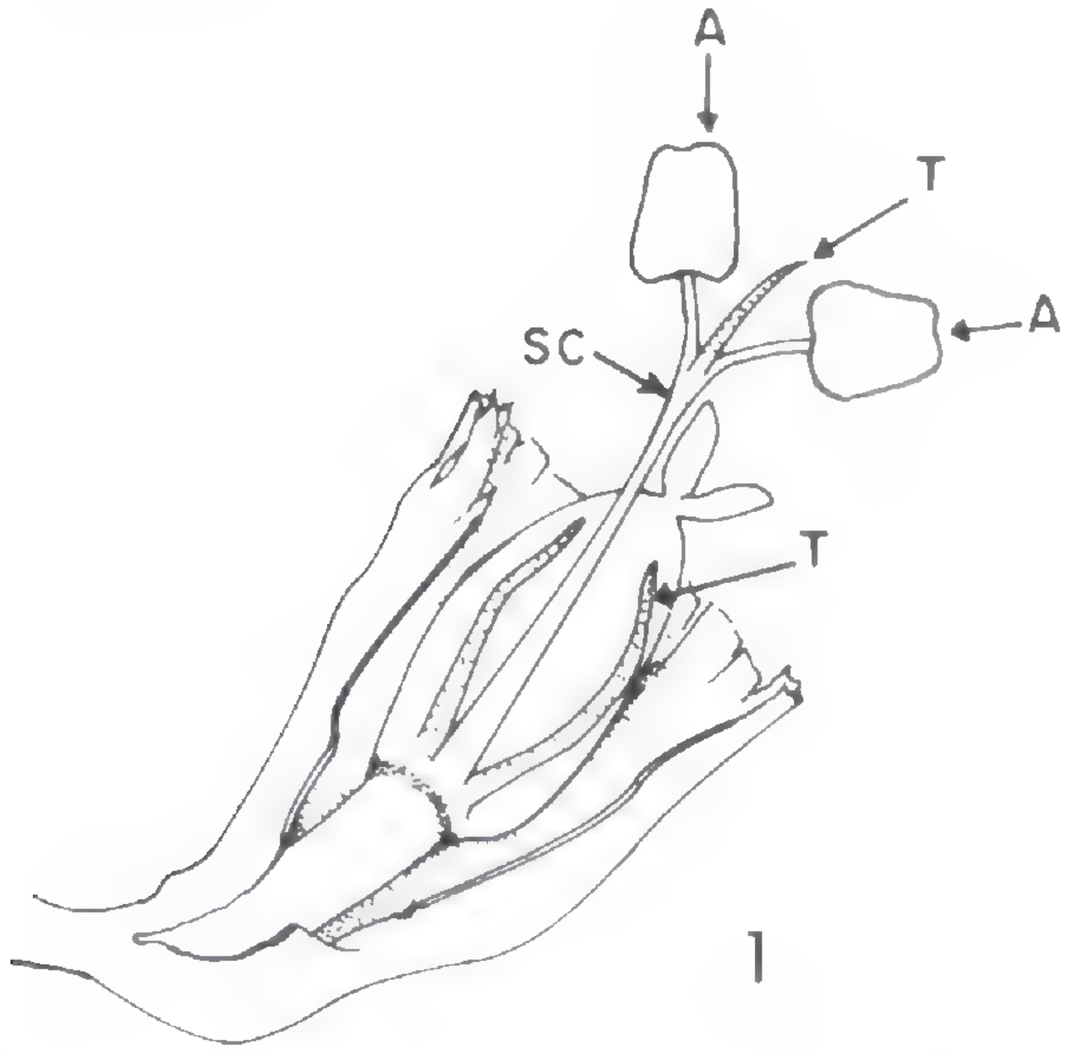
[2]Current address: Department of Ecology and Evolutionary Biology, U-43. The University of Connecticut, Storrs, CT 06268.

a superficial understanding of their overall biology has been achieved.

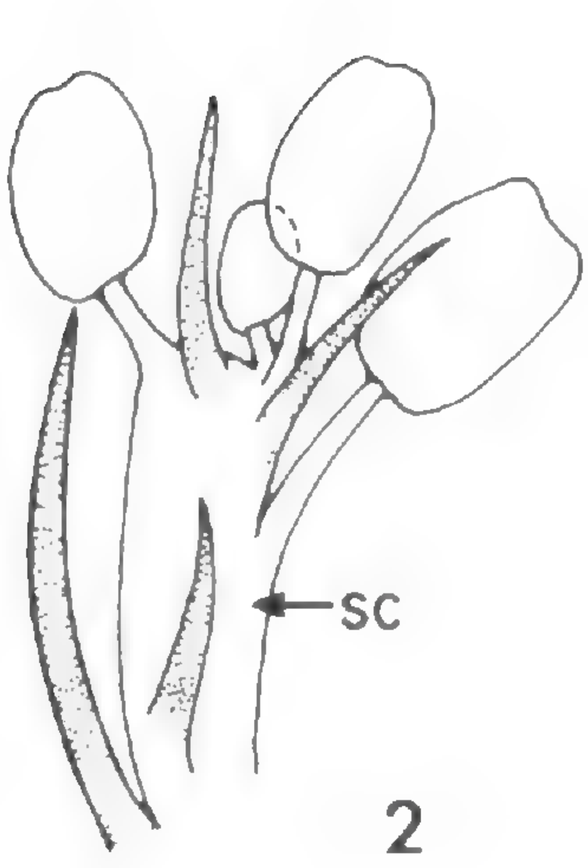
The family is represented in temperate regions by several species of *Cladopus* Möller and *Hydrobryum* Endl. in Japan (Ohwi, 1965) and by *Podostemum ceratophyllum* Michx. in eastern North America (Meijer, 1976; Philbrick, 1984; Philbrick & Crow, 1983). The purpose of this paper is to present evidence of previously undescribed variation in the floral morphology of *P. ceratophyllum* in the northeastern United States.

Variation in floral morphology (i.e., extra or morphologically distorted sepals, petals, stamens or carpels) occurs in many angiosperm genera. Additional floral organs may appear in all whorls at once, maintaining a regular floral symmetry, or in only one or two whorls, altering the basic symmetry. In some cases such polymorphism may be related to inbreeding, directional selection and environmental stress, factors that result in developmental instability in small populations isolated on the periphery of a species border. Interspecific hybridization may also result in polymorphism in peripherally isolated populations (Levin, 1970). The amount of abnormal merism within individual plants, or within and among populations, is usually not well documented, but has been studied in some taxa (Ellstrand, 1983; Levin, 1970). *Podostemum ceratophyllum* has not previously been studied in this regard.

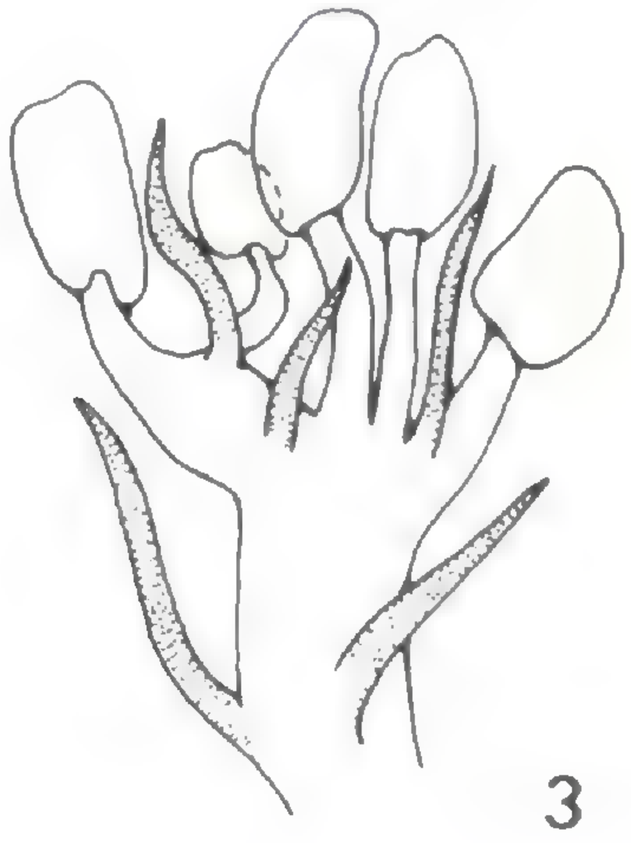
The zygomorphic flowers of *Podostemum ceratophyllum* (Figure 1) typically consist of a superior, two-carpelled, compound ovary; two stamens borne on a staminal column (the androphore, androdium, or fused filaments of various authors) that is adaxially and hypogynously inserted; and two or three awl-shaped tepals (Royen, 1954; Graham & Wood, 1975). The tepals have been interpreted as staminodes (Hammond, 1937) and are inserted laterally at the base of the androecium or on the staminal column (Figures 1–5). In the latter case a single tepal is often inserted at the sinus where two individual filaments become distinct from the staminal column (Figure 1). The tepal inserted at the fork of the staminal column was termed a "scale" by Hammond (1937). In this paper no distinction is made between tepals inserted on either side of the staminal column and those inserted on the column itself, because various intermediate conditions have been observed. The morphological nature of the tepals is unclear and their developmental anatomy has not yet been studied.



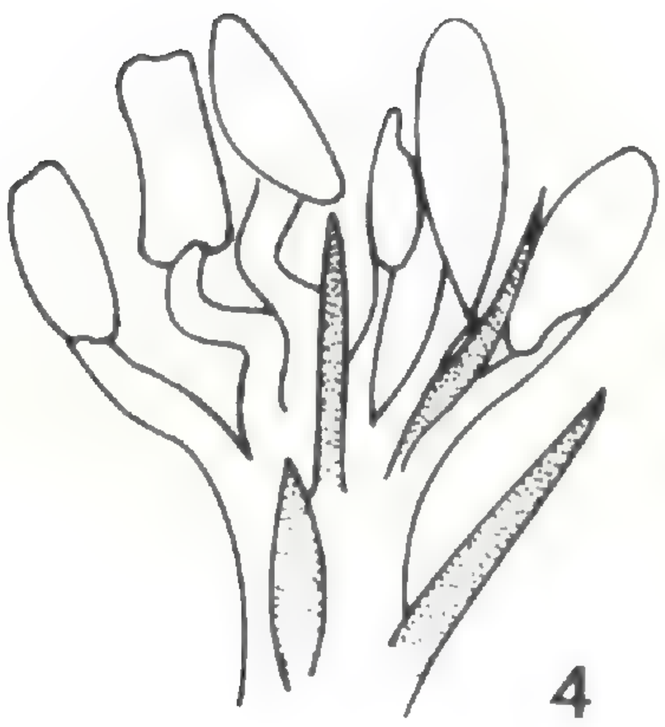
1



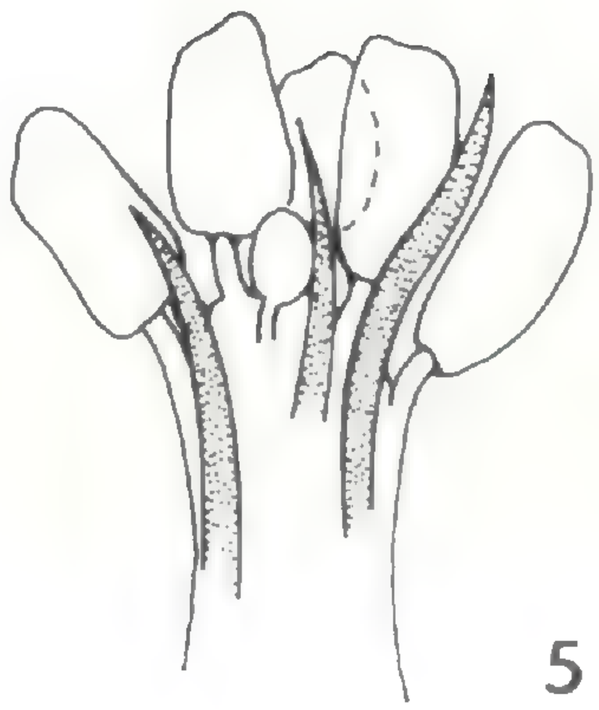
2



3



4



5

Figures 1–5. Typical flower, and variation in the androecium, of *Podostemum ceratophyllum*. **1.** Idealized diagram of a typical flower illustrating the position of the staminal column (SC), the number of tepals (T), and the number of anthers (A). **2–5.** Idealized diagrams of androecia of four flowers from the Kennebunk, ME population, illustrating the variation in number and position of tepals and anthers in the androecium.

Variations from the basic floral pattern previously reported for *Podostemum ceratophyllum* (Hammond, 1937; Royen, 1954; Graham & Wood, 1975) involved relatively minor differences in the number of anthers (2–3) or tepals (2–3). Philbrick (1982b) reported more extensive variation in floral organization (anther and tepal numbers ranged from 2 to 7) for a population of *P. ceratophyllum* at Kennebunk, Maine. The present investigation was undertaken to compare floral variation among several populations of *P. ceratophyllum* in order to reach a better understanding of the extent of variation in the species, and of temperate Podostemaceae in general. In addition, these data could be helpful in the formulation of subsequent investigations aimed at assessing what influence such variation has on the population biology of the species.

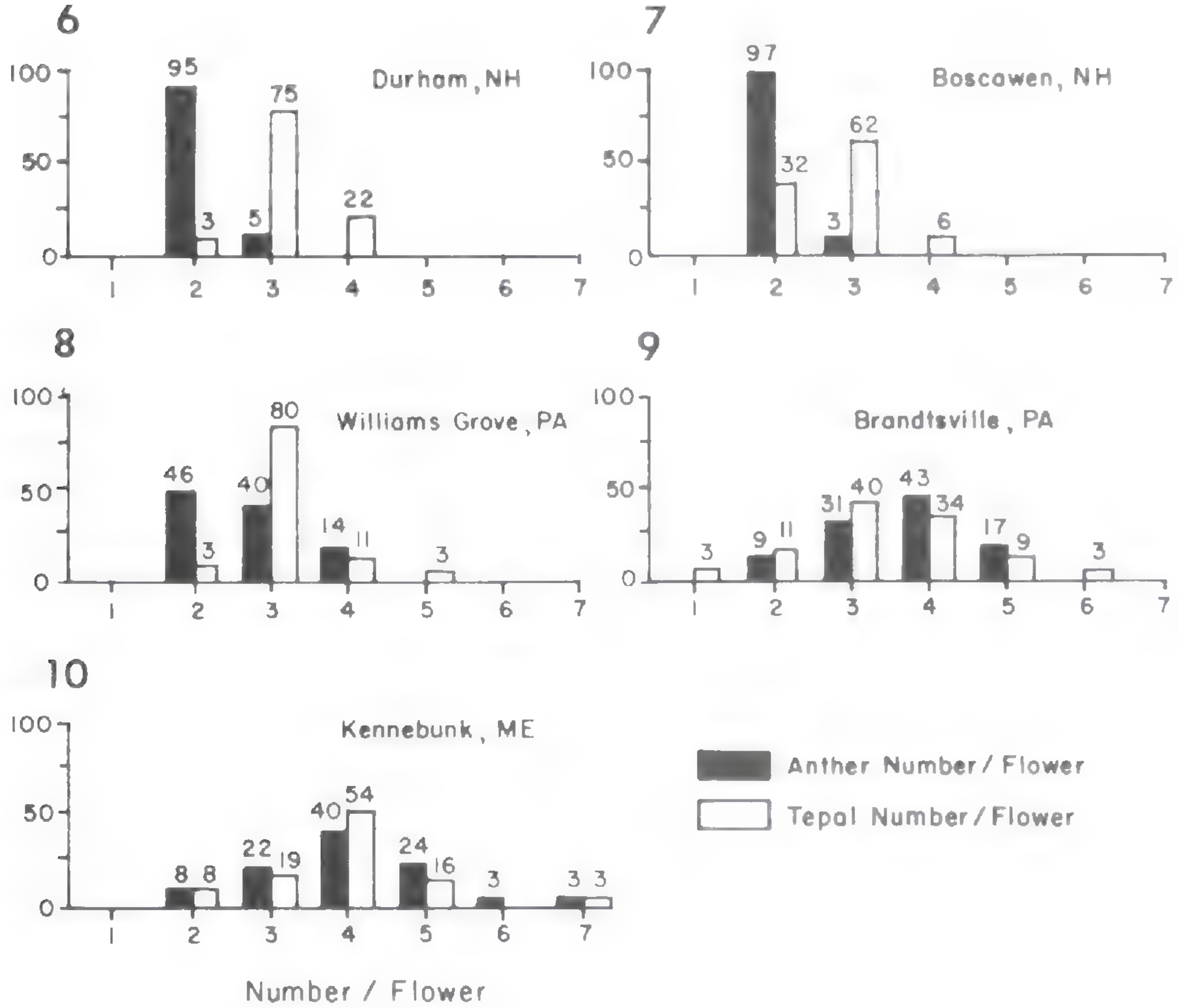
MATERIALS AND METHODS

Material was collected during the summers of 1981 and 1982 from populations at: Lamprey River, Packers Falls, Durham, NH *(Philbrick 1101);* Contoocook River, Boscawen, NH *(Philbrick 1100);* Yellow Britches Creek, Brandtsville, PA *(Philbrick 1165);* Yellow Britches Creek, Williams Grove, PA *(Philbrick 1166)* and Mousam River, Kennebunk, ME *(Philbrick 1137).* Voucher specimens are deposited at NHA. All specimens were preserved in FAA (formalin (5%) : glacial acetic acid (5%) : 70% ethanol (90%)). Samples of 75 randomly selected flowers from each population, three flowers from each of 25 stems, were examined.

To test for possible environmental influence on floral form, selected transplants between populations were conducted. Five rocks with their attached plants were removed from the Durham population in July, 1981, and transferred to the Kennebunk population. Flowers were collected from these plants before (June, 1981) and after (August, 1982) transplanting. Reciprocal transplants (Kennebunk to Durham) were also conducted, but flowers did not form on these plants during the summer of 1982.

RESULTS

Considerable variation was found in anther and tepal number per flower. However, the range of variation differed between populations. Flowers from the Durham and Boscawen populations exhibited the least amount of variation in anther number (Figures 6, 7); only 5% of the Durham sample and 3% of the Boscawen sample showed deviations (both with three anthers) from the typical two-anthered condition. Anther number was more variable in samples



Figures 6–10. Histograms showing variation in anther and tepal number per flower (indicated as the percent of total sample) from five populations of *Podostemum ceratophyllum*. **6.** Durham, NH **7.** Boscawen, NH **8.** Williams Grove, PA **9.** Brandtsville, PA **10.** Kennebunk, ME.

from Williams Grove, PA., Brandtsville, PA., and Kennebunk, ME. (Figures 8–10). Only 46% of the Williams Grove sample exhibited the typical two-anthered condition, while three- and four-anthered flowers made up 40% and 14% of the sample, respectively. The Brandtsville sample exhibited slightly more variation than that from Williams Grove, with two- (9%), three- (31%), four- (43%), and five- (17%) anthered flowers being observed (Figures 8, 9). Anther number varied most in the Kennebunk sample, where two- (8%), three- (22%), four- (40%), five- (24%), six- (3%), and seven- (3%) anthered flowers were present (Figure 10). Six and seven-anthered flowers were found only in the Kennebunk population.

The degree of anther development in each flower also varied considerably. This variation was especially evident in 5 to 7 anthered flowers, in which both normal anthers and poorly developed, distorted anthers were often observed in the same flower (compare

Figures 2 5). In each instance one of the anthers was noticeably smaller. Distorted anthers were often discolored, appearing grayish rather than the normal pinkish, but pollen stainability was comparable in normal and distorted anthers. A reduction in ovary size often accompanied an increase in anther number, especially in flowers with six or seven anthers. Ovary reduction may occur in response to crowding within the floral spathe because of the development of supernumerary anthers or tepals. Since the androecium matures before the gynoecium, presence of additional anthers may impede normal gynoecium development.

Variation in the number of tepals appeared to parallel that in anther number. The least variation was in the Durham and Boscawen samples, in which two to four tepals per flower were observed (Figures 6, 7) Greater variation occurred at Williams Grove, where two to five tepals per flower were found (Figure 8). As with anther number, the highest degree of variation in tepal number was at Brandtsville, PA., and Kennebunk, ME., where one to six, and two to seven tepals per flower, respectively, were observed (Figure 9, 10). In three (4%) of the flowers from Kennebunk, tepals were observed that bore what seemed to be rudimentary anthers. This condition could be interpreted as evidence that these organs are staminodial in origin, as proposed by Hammond (1937).

In addition to normal tepals occurring on the receptacle or staminal column, two other types of organs that cannot be interpreted in terms of typical floral structures were observed in eight (11%) flowers from the Kennebunk sample. In six flowers, green, dorsiventrally flattened, bract-like organs arose from the upper portion of the pedicel. These bodies lacked any uniformity in shape (ranging from linear to broader than long) or symmetry of insertion on the pedicel, and may represent vegetative structures. In two other flowers, linear, green, leaf-like organs arose low on the staminal column. When expanded these were much too long to be accommodated within the spathe, but had developed within the spathe by bending back on themselves several times. Their insertion on the staminal column suggests that they may represent elaborated tepals.

The Kennebunk population is the only one of the five examined that occurs in a noticeably polluted river (domestic sewage). We initially suspected that this pollution affected floral development and form. However, when plants were transplanted from the Durham population to the Kennebunk habitat, the floral form of the Durham plants was retained during the next growing season.

DISCUSSION

Variation in the number of anthers and tepals per flower reported here for *Podostemum ceratophyllum* exceeds any previously reported (Hammond, 1937; Royen, 1954; Graham & Wood, 1975). As we have shown, both anther and tepal number were least variable in the Durham and Boscawen populations (Figures 6–10). Anther number per flower in the Williams Grove sample was intermediate as compared to the other four populations. The Brandtsville sample showed considerably more variation in both anther and tepal numbers when compared to the Williams Grove, Durham and Boscawen samples, while the Kennebunk population exhibited the most variation in both of these traits. One might have expected greater similarity between the Williams Grove and Brandtsville populations than was observed, since they occur in the same river. Although a general tendency exists for flowers with larger numbers of anthers to possess additional tepals, presence of unusual floral structures in the Kennebunk population was not strongly correlated with presence of any other floral structure.

It is not known what factor(s) are responsible for the degree and pattern of variation of floral form that we observed. Further regional surveys and experimental investigations are certainly in order. Nonetheless, limited speculation as to possible explanations may be worthwhile. *Podostemum ceratophyllum* exhibits extensive vegetative growth via a system of prostrate axes which are usually interpreted as representing roots, and from which vegetative and flowering shoots arise (Engler, 1930; Hammond, 1937; Royen, 1954; Sculthorpe, 1967; Graham & Wood, 1975). Given the lack of seed production in many populations (Philbrick, 1981, 1984) vegetative reproduction is probably the major means of maintaining many populations. Vegetative fragments may also be a means of establishing new populations, especially downstream (Philbrick, unpublished data). Atypical floral forms established through processes such as mutation, inbreeding, directional selection and environmental stress (Levin, 1970) could be maintained in such asexually reproducing populations. In addition, in those populations that set seed, the autogamous pollination system (Philbrick, 1984) would also perpetuate a genetically based atypical floral form as long as the abnormality did not structurally or developmentally disrupt the autogamous system. That is, such modifications would not necessarily be selected against by discriminating biotic pollination vectors.

It is interesting that a somewhat similar range and pattern of variation is evident in populations in Maine and Pennsylvania. Although gene flow between these two areas is possible, it seems unlikely, especially via the sexual system. Establishment of one of these populations from a vegetative propagule dispersed from the other (or both from a common source) is also possible. Although we have difficulty in subscribing to this opinion we have little evidence to argue against it other than the seemingly great distance (ca. 500 miles) separating the populations. Further study is certainly needed to resolve this issue.

Philbrick (1982a, 1984) has reported that some populations of *Podostemum ceratophyllum* do not produce seed. Of the five populations considered here, only the Boscawen population is known to produce seed. The apparent cause of absence of seed-set in some populations is a lack of coincidence between anther maturation and stigma receptivity within the flower (Philbrick, 1982a). Fertility does not appear to be directly related to variation in floral morphology; i.e., populations with typical flowers may or may not produce seed. This conclusion is supported by the fact that of the two populations examined here with typical flowers (Boscawen and Durham), only one is known to produce seed (Boscawen).

On the basis of the available evidence presented here, including the distribution of floral polymorphism among different populations, our limited transplant studies, and current knowledge of the prevailing breeding systems, we conclude that genetic rather than environmental factors are the primary controlling influence on floral form in *Podostemum ceratophyllum*.

ACKNOWLEDGMENTS

We thank Gregory J. Anderson, Paula K. Busse and Thomas D. Lee, as well as several anonymous reviewers, for their helpful comments on this manuscript; we also thank Mary Jane Spring for Figures 1–10.

LITERATURE CITED

ELLSTRAND, N. C. 1983. Floral formula inconstancy within and among plants and populations of *Ipomopsis aggregata* (Polemoniaceae). Bot. Gaz. 144: 199–123.

ENGLER, A. 1930. Podostemonaceae. *In:* A. Engler & K. Prantl, Nat. Pflanzenfam, ed. 2. 18a: 1–68.

GRAHAM, S. A., AND C. E. WOOD, JR. 1975. The Podostemaceae in the southeastern United States. J. Arnold Arbor. 56: 456–476.

HAMMOND, B. L. 1937. Development of *Podostemum ceratophyllum*. Bot. Gaz 97: 834–845.

LEVIN, D. A. 1970. Developmental instability and evolution in peripheral isolates. Amer. Natur. 104: 343–353.

MEIJER, W. 1976. A note on *Podostemum ceratophyllum* Michx., as an indicator of clean streams in and around the Appalachian Mountains. Castanea 41: 319–324.

OHWI, J. 1965. Flora of Japan. Smithsonian Institution, Washington, D.C.

PHILBRICK, C. T. 1981. Some notes regarding pollination in a New Hampshire population of *Podostemum ceratophyllum* Michx. (Podostemaceae). Rhodora 83: 319–321.

———. 1982a. Reproductive biology of *Podostemum ceratophyllum*. *In*: Abstracts of papers presented at Pennsylvania State University. Bot. Soc. Amer. Misc. Publ. No. 162: 40.

———. 1982b. New locations for *Podostemum ceratophyllum* Michx. (Podostemaceae) in New Hampshire and Maine, with some comments on a unique floral form. Rhodora 84: 301–303.

———. 1984. Aspects of floral biology, breeding system, and seed and seedling biology in *Podostemum ceratophyllum* (Podostemaceae). Syst. Bot. 9: 166–174.

——— AND G. E. CROW. 1983. The distribution of *Podostemum ceratophyllum* Michx. (Podostemaceae). Rhodora 85: 325–341.

ROYEN, P. VAN. 1954. The Podostemaceae of the New World. Part III. Act. Bot. Neerl. 3: 215–263.

SCULTHORPE, C. D. 1967. The Biology of Aquatic Vascular Plants. St. Martins Press, New York.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
THE UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NH 03824

RHODORA, Vol. 90, No. 862, 1988

TYPIFICATION OF J. LUNELL'S NAMES IN *ADICEA* (URTICACEAE)

DAVID E. BOUFFORD

ABSTRACT

Type specimens are designated for J. Lunell's names in *Adicea* Rafinesque, *A. fontana, A. opaca, A. deamii* and *A. nieuwlandii,* all but one of which were based on multiple specimens. *Adicea deamii* and *A. nieuwlandii* are now considered synonyms of *Pilea pumila* (L.) A. Gray. *Adicea opaca* is considered synonymous with *A. fontana* under the name *Pilea fontana* (Lunell) Rydberg.

In 1913 J. Lunell described four new species of *Adicea* Rafinesque from North America, two black-fruited and two green-fruited. Rydberg (1931) transferred the specific epithets of the two black-fruited species from *Adicea* to *Pilea,* but did not account for the two green-fruited ones since they occurred outside his area of interest, the region covered by his *Flora of the Prairies and Plains of Central North America* (Rydberg, 1932). Fernald (1936) maintained one of the green-fruited species, *A. deamii* Lunell, as a variety of *P. pumila* (L.) A. Gray, but placed the other in synonymy under *P. pumila* var. *pumila.* Fernald, and later Hermann (1940), also recognized only a single black-fruited species. Lunell did not clearly indicate a type specimen for any of his new names; it is apparent from his handwritten "type" and "co-type" on some of the specimens used as the basis for the original descriptions that his type concept differed from that currently in use. Fernald mentioned examining an "isotype" of *Adicea deamii,* but in fact the specimen he saw in the Gray Herbarium was a syntype. I have just examined Lunell's specimens, which were acquired by MIN in 1927, and wish here to designate type specimens for each of his published names in *Adicea.*

Adicea fontana Lunell, Amer. Midl. Naturalist 3: 7. 1913.

LECTOTYPE, here chosen: NORTH DAKOTA, Benson County, Pleasant Lake, on a narrow strip along the narrow margin of a rill, in deep shade, 2 September 1912, *J. Lunell 336,* "Type" in lower right corner of label (MIN). Three additional sheets (MIN) collected by Lunell are numbered *336.* One, annotated "Co-type specimen no. 1," was collected on 3 July 1912. Another, annotated "Co-type specimen no. 2," was collected on 14 August 1911, and the third, without

any type status indicated, was collected on 28 July 1912. A fourth specimen (MIN), collected on the same date as the lectotype and annotated "Co-type," is *Lunell 634*. The label data differ in wording on each of the five sheets, including the two sheets collected on 2 September. *Adicea fontana* is now treated as *Pilea fontana* (Lunell) Rydberg (Brittonia 1: 87. 1931.).

Adicea opaca Lunell, Amer. Midl. Naturalist 3: 8. 1913.

LECTOTYPE, here chosen: NORTH DAKOTA, Benson County, in damp but drained soil, in the woodland at Pleasant Lake, 2 September 1912, *J. Lunell 337* (MIN; ISOLECTOTYPE: MIN). Both sheets are annotated "Type." A third sheet, annotated "Co-type" and collected on the same date, but with slightly different wording on the label, is *Lunell 635* (MIN). *Adicea opaca* (*Pilea opaca* (Lunell) Rydberg, Brittonia 1: 87.1931.) is treated as a synonym of *P. fontana*.

Adicea nieuwlandii Lunell, Amer. Midl. Naturalist 3: 10. 1913.

HOLOTYPE: INDIANA, Notre Dame, 19 October 1912, *J. A Nieuwland 10341* (MIN). This sheet appears to be the only one on which *A. nieuwlandii* was based and, although not stated as such in the protologue, it can be considered the holotype. *Adicea nieuwlandii* has always been treated as a synonym of *Pilea pumila;* the combination in *Pilea* has never been made.

Adicea deamii Lunell, Amer. Midl. Naturalist 3: 10. 1913.

LECTOTYPE, here chosen: INDIANA, Mineral Springs, 26 September 1912, *J. A. Nieuwland 10236* (MIN). The lectotype specimen has a small annotation label in the lower center of the sheet with "*Adicea Deamii* Lunell, sp. nov." handwritten in ink. "Type," in pencil, is handwritten on the original collection label. The second specimen cited by Lunell, Indiana, Wells County, rich moist woods in Lancaster Twp., sec. 16, 24 August 1902, *C. C. Deam s.n.* (MIN), has "*Adicea Deamii* Lunell, sp. nov." written in pencil on the original label. A duplicate of the second sheet, which Fernald called an isotype, is at GH. *Adicea deamii* is now generally treated as a synonym of *Pilea pumila,* although Fernald recognized it as *P. pumila* var. *deamii* (Lunell) Fernald (Rhodora 38: 169. 1936.).

ACKNOWLEDGMENTS

I thank Anita Cholewa for the loan of specimens of Urticaceae from MIN and two anonymous reviewers for their helpful comments.

LITERATURE CITED

FERNALD, M. L. 1936. *Pilea* in eastern North America. Rhodora 38: 169–170.
HERMANN, F. J. 1940. The geographic distribution of *Pilea fontana*. Torreya 40: 118 120.
LUNELL, J. 1913. *Adicea*. Amer. Midl. Naturalist 3: 6–12.
RYDBERG, P. A. 1931. Taxonomic notes on the flora of the prairies and plains of central North America. Brittonia 1: 79 104.
_____. 1932. Flora of the Prairies and Plains of Central North America. The New York Botanical Garden, New York.

HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

RHODORA, Vol. 90, No. 862, 1988

NEW CHROMOSOME COUNTS IN *ACER* (MAPLE) SPECIES, SECTIONS *ACER* AND *GONIOCARPA*

FRANK S. SANTAMOUR, JR.

ABSTRACT

Diploid chromosome counts ($2n = 26$) are reported for the first time in *Acer heldreichii* and *A. trautvetteri* (section *Acer*) and in *A. hyrcanum, A. opalus, A. pentapomicum,* and *A. syriacum* (section *Goniocarpa*). *Acer velutinum* (section *Acer*) was a newly discovered tetraploid ($2n = 52$). The diploid numbers of *A. caesium* (section *Acer*) and *A. monspessulanum* (section *Goniocarpa*) and the tetraploid number of *A. pseudoplatanus* (section *Acer*) were confirmed. Chromosome counts may now be used to verify suspected hybrids between diploid and tetraploid taxa.

Key Words: cytology, cytotaxonomy

INTRODUCTION

Correct delineation of infrageneric taxonomic classes, especially in complex genera such as *Acer* (maple), is important both to systematists and geneticists. Based on limited studies of controlled pollination, each botanical section in *Acer,* as recognized by Delendick (Ph.D. thesis, CCNY, 1981), appears to constitute a separate germplasm pool. Interspecific hybrids are possible between species in the pool but intersectional crosses are practically impossible to accomplish. The earlier taxonomic treatment of *Acer* by Pax (1902), used by Rehder (1940), was not sufficiently precise at the sectional level to use as a guide to potential crossing abilities.

Proper classification was especially critical in sections *Acer* and *Goniocarpa,* where a number of natural or garden-origin hybrids involving species belonging to these two sections had been described. Murray (Ph.D. thesis, Penn. State Univ., 1970) listed hybrids of *A. pseudoplatanus* L. with *A. heldreichii* Orph. ex Boiss. and *A. monspessulanum* L., and also unverified intersectional hybrids between *A. campestre* L. (section *Platanoidea*) and *A. monspessulanum, A. opalus* Mill., and *A. pseudoplatanus.*

Cytological knowledge of the species in these sections was inadequate (in 1981–82) to use as a taxonomic tool, but the distribution of polyploids in the genus *Acer* suggested that such studies might be extremely useful. All three of the species in section *Rubra* are polyploid (Santamour, 1965, 1971) as is the single species *A. carpinifolium* Sieb. & Zucc. in section *Indivisa* (Taylor, 1920). The only other

polyploid ($4x = 2n = 52$) species reported in the genus was *A. pseudoplatanus* (Taylor, 1920; Foster, 1933), the type species for the genus and for section *Acer*. The only other known (and uncontested) chromosome count in either section *Acer* or section *Goniocarpa* was the diploid ($2n = 26$) determination for *A. monspessulanum* of section *Goniocarpa* (Lovka et al., 1971). The present study was undertaken to make chromosome counts on other taxa in sections *Acer* and *Goniocarpa* and to determine if polyploidy could be used as a basis for distinguishing these sections.

This work was given added impetus by our early finding that *Acer velutinum* Boiss. of section *Acer* was a tetraploid, and the possibility that *A. caesium* Wall. ex Brandis (section *Acer*) was also a tetraploid. *Acer caesium* had been reported both as a diploid and a tetraploid but the road to the tetraploid count is tortuous indeed. Mehra and Sareen (1969) listed the species as a diploid with $n = 13$ chromosomes; the same number is listed in Mehra et al. (1972). These works were referenced by Moore (1971, 1977) in his indices to plant chromosome numbers. Mehra (1976), recognizing the many and varied times and places of publication of his and his associates' prodigious cytological work on Himalayan hardwoods, compiled these investigations into a single volume. In the list on page XXI of the introduction to that work, *A. caesium* is again reported as having $n = 13$ chromosomes, but in the text (p. 47) it was stated that "Twenty-six bivalents along with a nucleolus were observed at diakinesis" and again (p. 52) "Excepting *A. caesium* which is tetraploid with $n = 26$. . ." Furthermore, in the listing, the diploid count was apparently corroborated as $2n = 26$ by "Takizawa, 1953," but there is no reference provided for this work. Apparently, in the midst of the mass of plants and data accumulated by Mehra and his coworkers, *A. caesium* lost its way, at least temporarily.

MATERIALS AND METHODS

Beginning in the spring of 1985, an attempt was made to secure and study authentic plant material of all maple species classified in sections *Acer* and *Goniocarpa*. When possible, meiosis in the pollen mother cells or mitosis in root tips was studied. However, because of the scarcity of most of these taxa in cultivation, most of the counts were made at mitosis in the early-breaking leaf buds of twigs shipped to this laboratory during the dormant season and forced into growth with heat, light, and moisture in the greenhouse or laboratory. Several species required alternating cold and warm

periods to stimulate bud break. Leaf tissue was treated with 0.1% colchicine for 3 hours, killed and fixed in 1:3 acetic-alcohol, hydrolyzed in 1N HCL, and squashed in acetocarmine. Sources, accession numbers, and other information regarding the individual plants studied are given in "Results," coded as follows: (AA) Arnold Arboretum of Harvard University, Jamaica Plain, MA; (LA) Los Angeles State and County Arboretum, Arcadia, CA; (NA) U.S. National Arboretum, Washington, D.C.; (UG) University of Guelph Arboretum, Guelph, Ontario, Canada; and (UW) University of Washington Arboretum, Seattle, WA. Plant Introduction (PI) numbers are those assigned by the U.S. Department of Agriculture. Living plants and herbarium specimens are located at the institutions of origin.

RESULTS

Section Acer

A. caesium Wall. ex Brandis

Diploid: $2n = 26$ in leaves of UW 779–60.

A. heldreichii Orph. ex Boiss.

Diploid: $2n = 26$ in leaves of AA 5759 and var. *macropterum* (Visiani) Pax AA 12498.

A. pseudoplatanus L.

Tetraploid: $n = 26$ at meiosis in NA 2836, plant from Kohankie and Sons, Painesville, OH, 1941; $n = 26$ in cv. Purpureum (Atropurpureum) NA 9631, plant from Sussex Nurs., Bridgeville, DE, 1957; $2n = 52$ in seedling of NA 9631.

A. trautvetteri Medwed.

Diploid: $2n = 26$ in leaves of UG 73 -43–1 and –2, UW 695–60.

A. velutinum Boiss.

Tetraploid: $2n = 26$ at meiossi in var. *vanvolxemii* (Mast.) Rehd., NA 21700, PI 277758; $2n = 52$ in root tips of var. *glabrescens* (Boiss. & Buhse) Rehd., AA 983–78 (rooted cuttings of AA–381–77).

Section Goniocarpa

A. hyrcanum Fisch. & Mey.

Diploid: $2n = 26$ in leaf of AA 31–73–C, UG 73–1739–1.

A. opalus Mill.

Diploid: $2n = 26$ in root tips of NA 35075, PI 377769 and NA 35076, PI 377770, rcd. as seed of var. *obtusatum* (Willd.) Henry from Yugoslavia.

A. pentapomicum Stewart ex Brandis

Diploid: $2n = 26$ in leaves of UW 48–70. This species may also be classified in section *Pubescentia* (Delendick, Ph.D. thesis, CCNY, 1981).

A. syriacum Boiss. & Gaill.

Diploid; $2n = 26$ in leaves of LA 68–S–521. Annotated as *A. orientale* Sm. ssp. *syriacum* (Boiss. & Gaill.) E. Murray by E. Murray.

DISCUSSION

These new data on chromosome numbers do not, unfortunately, shed any new light on the classification of species in sections *Acer* and *Goniocarpa*. However, it is obvious that all species of a given section need not possess the same ploidy level, as might have been assumed before this work. One new tetraploid taxon (*Acer velutinum*) was found, but the diploid counts are of equal importance. Chromosome counts can now be used as verification of hybrids, intrasectional or intersectional, between diploid and tetraploid taxa.

ACKNOWLEDGMENTS

Many thanks are extended to the directors and personnel of the institutions mentioned herein as sources for plant material.

LITERATURE CITED

Foster, R. C. 1933. Chromosome number in *Acer* and *Stephylea*. J. Arnold Arbor. 14: 386–393.

Lovka, M., F. Susnik, A. Love, and D. Love. 1971. *In:* I O P B chromosome number reports XXXIV, A. Love, Ed. Taxon 20: 785–797.

Mehra, P. N. 1976. Cytology of Himalayan Hardwoods. Sree Saraswaty Press, Calcutta.

———, P. K. Khosla, and T. S. Sareen. 1972. Cytogenetical studies of Himalayan Aceraceae, Hippocastanaceae, Sapindaceae, and Staphyleaceae. Silvae Genet. 21: 96–102.

——— and T. S. Sareen. 1969. *In:* I O P B chromosome number reports XXII, A. Love, Ed. Taxon 18: 433 442.

Moore, R. J., Ed. 1971. Index to Plant Chromosome Numbers for 1969. Regnum Vegetabile Vol. 77.

———. 1977. Index to Plant Chromosome numbers for 1973/74. Regnum Vegetabile Vol. 96.

Pax, F. 1902. Aceraceae. *In:* A. Engler, Das Pflanzenreich IV, 163, 8: 1–89.

Rehder, A. 1940. Manual of Cultivated Trees and Shrubs Hardy in North America. (ed. 2), Macmillan. New York.

SANTAMOUR, F. S., JR. 1965. Cytological studies in red and silver maples and their hybrids. Bull. Torrey Bot. Club 92: 127–134.

_____. 1971. *In:* I O P B Chromosome number reports XXXII, A. Love, Ed. Taxon 20: 349–356.

TAYLOR, W. R. 1920. A morphological and cytological study of reproduction in the genus *Acer*. Contrib. Bot. Lab. Morris Arbor. Univ. Pennsylvania 5(2): 111–138.

U.S. NATIONAL ARBORETUM
USDA, AGRICULTURAL RESEARCH SERVICE
WASHINGTON, D.C. 20002

RHODORA, Vol. 90, No. 862, 1988

THE GENUS *ANTENNARIA* (ASTERACEAE: INULEAE) IN WESTERN NORTH AMERICA. II. ADDITIONAL CHROMOSOME COUNTS

J. G. Chmielewski and C. C. Chinnappa

ABSTRACT

Chromosome numbers were determined from somatic material for 153 individuals representing 16 taxa from western North America. First counts ($2n = 56, 70$) are reported for *Antennaria stolonifera* Porsild. The remaining counts ($2n = 28, 42, 50, 60, 70, 112$, ca. 120, ca. 130, and ca. 140) support previous reports and are presented without comment.

Key Words: *Antennaria,* chromosome counts, western North America

INTRODUCTION

The chromosome number(s) of a taxon may be used to determine whether a species is uniform throughout its range, to determine the amount and nature of the diversity (Mosquin and Hayley, 1966), to define the limits of distribution of infraspecific variants, to reconstruct biogeographic histories, and to determine the evolution of infraspecific polyploidy (Semple et al., 1983). The chromosome numbers of some western North American *Antennaria* Gaertner have been determined over part of their ranges (Johnson and Packer, 1968; Packer and McPherson, 1974; Bayer and Stebbins, 1981, 1987; Urbanska, 1983; Bayer, 1984; Chinnappa, 1984, 1986; Chmielewski and Chinnappa, in press). Chinnappa (1984) reported the first triploid counts in the genus. The present investigation reports chromosome number determinations for 16 taxa in western North America. Taxonomic notes are included for *A. stolonifera* for which chromosome numbers have not been previously reported. Chromosome number determinations are presented for the remaining taxa without comment.

METHODS AND MATERIALS

Cultivation of specimens and preparation of somatic material for chromosome number determinations followed the procedures of Chinnappa (1986). We report the chromosome number(s) separately for taxa which may eventually be shown to represent minor variants

or possible microspecies. This procedure was not aimed at lending support to the taxonomic recognition of these variants, but rather as an informative aid to those presently working on these unrevised species complexes. All vouchers were collected by members of this laboratory and were subsequently deposited at UAC.

RESULTS AND DISCUSSION

Chromosome numbers were determined for 153 individuals representing 16 taxa (Table 1) and are reported separately for pistillate and staminate clones. First counts are reported for *Antennaria stolonifera* Porsild. All other counts confirm previous reports for the respective taxa and are presented to supplement our knowledge relative the chromosome number distribution.

The populations of *Antennaria stolonifera* from southwestern Alberta which we examined may be confused with *A. alpina* var. *media*. These would, however, be atypical forms of the latter. Variation in growth form of flowering heads, number of flowers and phyllary coloration allow for the confident separation of these species. The flowering heads of *A. stolonifera* occur on short (1–3 cm long) peduncles. As the flowering heads mature, the lateral peduncles elongate so that they either become equal in length to or overtop the central heads. Flowering occurs between June and mid-August. The species typically occupies alpine slopes but may also be found mixed with grass species along forest margins. It is locally common in central Alaska and central and southeast Yukon; it also occurs on the east slope of the Mackenzie Mountains (Porsild and Cody, 1980), and extends south through the Canadian Rockies, just entering the United States in northern Washington State (Chmielewski and Chinnappa, at review). The chromosome numbers ($2n$ = 56, 70) of this species have not been previously reported.

Table 1. Chromosome number determinations in *Antennaria* from western North America; numbers are reported for pistillate clones unless otherwise indicated. Voucher specimens were collected by C. C. Chinnappa unless indicated otherwise: BS = B. Smith; HF = H. Friebe.

A. alborosea Porsild. $2n = 56$. **Alberta:** Jasper National Park, Maligne Lake, *2670*.

A. alpina (L.) Gaertn. $2n = 56$. **Alberta:** Banff National Park, Parker Ridge, *2723, 2729, 2730*. Mount Norquay Ski Resort, *2739*. Jasper National Park, Maligne Lake, *2674, 2675*. Angel Glacier, *2707*. $2n = 70$. **Alberta:** Banff National Park, Parker Ridge, *2728*. $2n = 112$. **Alberta:** Jasper National Park, Maligne Lake, *2680*. Angel Glacier, *2705*. $2n$ = ca. 120. **Alberta:** Banff National Park, Mount Norquay Ski Resort, *2735*.

A. anaphaloides Rydb. (staminate) $2n = 28$. **Colorado:** dirt trail between Meeker and Craig, east of Hwy. 13, 27 km N of Rifle, *2081*.

A. Laingii Porsild. $2n = 56$. **Alberta:** Banff National Park, Parker Ridge, *2722*. Lake Minnewanka Rd, 1 km W of Two Jacks Campground *2744*.

A. lanata (Hook.) Greene. $2n = 28$. **Alberta:** Banff National Park, Parker Ridge, *2721*.

A. marginata Greene. $2n = 112$. **Arizona:** AZ 89, milepost 383, 36 km N of Sedona, *1980*.

A. microphylla Rydb. $2n = 28$. **Alberta:** Banff National Park, Lake Minnewanka Rd., 1 km W of Two Jacks Campground, *2743*. Jasper National Park, Maligne Lake Rd., Park Wardens Office, *2669*. 1.6 km E of Pocahontas, *2693*. Yellowhead Hwy., 4.8 km W of Jasper, *2694*. Hwy. 93A, S of Jasper, Marmot Basin, *2698, 2700, 2702*. **Colorado:** Hwy. 24, 7 km N of Leadville, *2070*. **Manitoba:** Hwy. 478, 3 km E of Saskatchewan, *BS691*. **Saskatchewan:** Hwy. 9, 1 km W of Flaxcombe, *BS631*. Hwy. 9, 6 km W of Herschel, *BS634*. Route 41, 11 km SW of Aberdeen, *BS643*. Junction of Hwy. 2 and Hwy. 25, St. Louis, *BS651, BS652*. Hwy. 2, 15 km S of Prince Albert, *BS654*. Hwy. 2, N of Prince Albert, *BS656*. Sandy Lake, Prince Albert National Park, *BS666*. Hwy. 35, 4 km N of Sylvania, *BS668*. Archerwill, *BS670*. Leslie Beach, Joan Lake, *BS672*. Hwy. 10, turnoff to Calder, *BS674*. Hwy. 22, 4 km E of Lemberg, *BS694*.

A. microphylla Rydb. (staminate) $2n = 28$. **Alberta:** Jasper National Park, Maligne Lake Rd, Park Wardens Office, *2668*. 3.2 km W of Rocker R., Pocahontas, *2668*. 1.6 km E of Pocahontas, *2692*. **Manitoba:** Hwy. 5, 12 km E of Robbin, *BS679*. 3 km W of Dauphin, *BS683*. 10 km E of Shoal Lake, *BS686*. Hwy. 478, 3 km E of Saskatchewan, *BS690*. **Saskatchewan:**Hwy. 2, Wakaw, *BS650*.15 km S of Prince Albert, *BS653*. Hwy. 2, N of Prince Albert, *BS655*. Sandy Lake, Prince Albert National Park, *BS665*. 4 km N of Sylvania, *BS667*. Archerwill *BS669*. Hwy. 10, turnoff to Calder, *BS673*. 1 km W of Stockholm, *BS692*. Hwy. 22, 4 km E of Lemberg, *BS693*. Route 10, 9 km NE of Balgonie, *BS695*.

A. monocephala DC. $2n = 56$. **Alberta:** Banff National Park, Parker Ridge, *2725*. $2n = 70$. **Alberta:** Jasper National Park, Angel Glacier, *2708*.

A. neodioica Greene. $2n = 112$. **Alberta:** Jasper National Park, Maligne Canyon trail, *2684*. Yellowhead Hwy., 4.8 km W of Jasper, *2695*.

A. neodioica Greene. ssp. *howellii* (Greene) Bayer. $2n = 70$. **Alberta:** Banff National Park, Lake Minnewanka Rd, 1 km W of Two Jacks Campground, *2745*. $2n = 112$. **Alberta:** Jasper National Park, Maligne Lake, *2683*.

A. parvifolia Nutt. $2n = 70$. **Alberta:** Jasper National Park, Maligne Canyon, *2682*. $2n = 112$. **Arizona:** Hannigan Meadow Forest Campground, 0.8 km S of Hannigan, *2003*. 5 km N of Sheeps Crossing–Lee Valley Recreational Area, *2022, 2030*. **Colorado:** San Juan National Forest, Hwy. 160 MP111, *2040, 2049*. **Montana:** Pine River Rd., 1 km E of Hwy. 59, 16 km S of Livingstone, *2132*. **Saskatchewan:** Hwy. 4, just N of Rosetown, *BS638*. Route 376, Eagle Creek Regional Park, *BS641*. Hwy. 2, N of Prince Albert, *BS658*. **Wyoming:** Rockefeller Pkwy, 0.5 km N of S entrance to Grand Teton National Park, *2111*. Yellowstone National Park, Old Faithful Geyser, *2120*. $2n =$ ca. 120. **Manitoba:** Hwy. 5, 11 km E of Robbin, *BS678*. Hwy. 270, near Riding Mountain National Park, *BS685*. $2n =$ ca. 130. **Alberta:** Jasper National Park, Maligne Canyon trail, *2685*. **Colorado:** Hwy. 24, 1 km S of Granite, *2064*. Hwy. 13, 27 km N of Rifle, *2083*. **Saskatchewan:** Hwy. 9, 6 km W of Herschel, *BS635*. **Wyoming:** Yellowstone National Park, Old Faithful Geyser, *2124*. $2n =$ ca. 140. **Manitoba:** Hwy. 5, 12 km E of Robbin, *BS681*.

A. parvifolia Nutt. (staminate) $2n = 112$. **Colorado:** San Juan National Forest, E of Bayfield, *2041, 2042.*

A. rosea Greene. $2n = 42$. **Alberta:** Banff National Park, Rd. to Mt. Norquay Ski Resort, *2738.* **Colorado:** Hwy. 13, 27 km N of Rifle, *2082.* **Montana:** Pine River Rd., 1 km E of Hwy. 59, 16 km S of Livingstone, *2131.* **Wyoming:** Yellowstone Pkwy., Mammoth Hot Springs, *2129.* $2n = 56$. **Alberta:** Banff National Park, Lake Louise Ski Resort, *2137.* Moraine Lake, 11 km S of Lake Louise, *2718.* Protection Mountain Campground, 3 km SE of Baker Ridge, *2719.* Mount Norquay Ski Resort, *2736, 2737.* Lake Minnewanka Rd., 1 km W of Two Jacks Campground, *2740.* Jasper National Park, Maligne Lake, *2671, 2673, 2677, 2678, 2681.* Maligne Lake Rd., Park Wardens Office, *2672.* Maligne Canyon trail, *2686.* Yellowhead Hwy., 4.8 km W of Jasper, *2696.* Hwy. 93A, S of Jasper, Marmot Basin, *2699.* Jnct. Icefields Pkwy. and Hwy. 93A, 30 km S of Jasper, *2709.* Sunwapta Falls, Icefields Pkwy., *2712, 2713.* **British Columbia:** 14 km E of Lone Butte, *HF5.* **Colorado:** Hwy. 24, 1 km S of Granite, *2062, 2063.* Hwy. 24, 7 km N of Leadville, *2065, 2066.* Rocky Mountain National Park, Hwy. 34, *HF21.* **Idaho:** Twin Creek Campground, 8 km N of Gillingsham, *HF27.* **Montana:** Allen Gulch Rd., Lewis Clark National Forest, *2133.* Hwy. 89, S of Neihart, *HF2.* **Utah:** Hwy. 91, Ashley National Forest, *HF26.* **Wyoming:** Hwy. 789 near Creston, *2087.* Hwy. 189, 23 km S of boundary to Teton National Forest, *2095.* Hwy. 189, 42 km S of Jackson, *2096.* S of Teton National Forest, Hoback junction, *2099.* 11 km N of Glacier Gulch scenic lookout, *2105.* Grand Teton National Park, 2 km N of Jenny Lake junction, *2106, 2107.* Rockefeller Pkwy., 1 km S of Pilgrim Creek Rd. *2108, 2109, 2110.* Rockefeller Pkwy., 1 km N of Yellowstone National Park, *2117, 2118.* Old Faithful Geyser, *2125.* Indian Creek Campground, *HF4A, B, 5A.* Snake River Campground, *HF9.* $2n = 60$. **Wyoming:** Medicine Bow National Forest, Last Creek Campground, *HF14.* 3 km E of Ryan Park, *HF16.* $2n = 70$. **Alberta:** Banff National Park, Moraine Lake, 11 km S of Lake Louise, *2716.*

A. rosea Greene. (staminate) $2n = 56$. **Montana:** Pine River Rd, 1 km E of Hwy. 59, 16 km S of Livingstone, *2130.* **Wyoming:** Hwy. 189, 42 km S of Jackson, *2094.* Rockefeller Pkwy., 1 km N of Yellowstone National Park, *2116.* Yellowstone National Park, Old Faithful Geyser, *2119, 2121, 2123.* Rockefeller Pky., 7 km S of Madison, *2126, 2127.*

A. rosulata Rydb. $2n = 28$. **Arizona:** 31 km W of AZ 89A and I 40, between Williams and Flagstaff, *1975.*

A. rosulata Rydb. (staminate) $2n = 28$. **Arizona:** 31 km W of AZ 89A and I 40, between Williams and Flagstaff, *1976.*

A. sedoides Greene. $2n = 60$. **Alberta:** Banff National Park, Parker Ridge, *2727.*

A. stolonifera Porsild. $2n = 56$. (first count). **Alberta:** Banff National Park, Lake Louise Ski Resort, *2135, 2136.* Jasper National Park, Maligne Lake, *2679.* $2n = 70$. **Alberta,** Banff National Park, Lake Louise Ski Resort, *2139.* Moraine Lake, 11 km S of Lake Louise, *2717.*

A. umbrinella Rydb. $2n = 28$. **Wyoming:** Jackson airport Rd., 12 km N of Teton National Forest, *2103.* $2n = 56$. **Wyoming:** Hwy. 189, 42 km S of Jackson, *2093.* Yellowstone National Park, Bridge Bay, *HF7.*

A. umbrinella Rydb. (staminate) $2n = 56$. **Wyoming:** Jackson airport Rd., 12 km N of Teton National Forest, *2104.*

ACKNOWLEDGMENTS

We thank Dr. B. G. Warner, H. Friebe, C. Leuty, B. Purdy, and B. Smith for their assistance in the field. National Parks collection permits were kindly issued for Banff and Jasper National Parks by Parks Canada (Western Region), and the United States Department of the Interior (National Park Service) for Yellowstone and Grand Teton National Parks. This work is supported by an operating grant (No. A7222) to CCC from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). Syst Bot. 9: 74–83.

_____ AND G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). Amer. J. Bot. 68: 1342–1349.

_____ AND _____. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). Syst. Bot. 2: 305–319.

CHINNAPPA, C. C. 1984. Triploidy in the genus *Antennaria* (Asteraceae: Inuleae) Canad.J Genet. Cytol. 26: 133–136.

_____. 1986. Chromosome numbers in *Antennaria* (Asteraceae: Inuleae) from western North America. Canad. J. Genet. Cytol. 28: 468–475.

CHMIELEWSKI, J. G. AND C. C. CHINNAPPA. Taxonomic notes and chromosome numbers in *Antennaria* Gaertner (Asteraceae: Inuleae) from arctic North America. Arctic and Alpine Res. (In press).

JOHNSON, A. W. AND J. G. PACKER. 1968. Chromosome numbers in the flora of Ogotoruk Creek, N.W. Alaska. Bot. Not. 121: 403–456.

MOSQUIN, T. AND D. E. HAYLEY. 1966. Chromosome numbers and taxonomy of some Canadian Arctic plants. Canad. J. Bot. 44: 1209–1218.

PACKER, J. G. AND G. D. MCPHERSON. 1974. Chromosome numbers in some vascular plants from northern Alaska. Canad. J. Bot. 52: 1095–1099.

PORSILD, A. E. AND W. J. CODY. 1980. Vascular Plants of Continental Northwest Territories, Canada. National Museums of Canada, Ottawa.

SEMPLE, J. C., J. G. CHMIELEWSKI AND C. C. CHINNAPPA. 1983. Chromosome number determinations in *Aster* L. (Compositae) with comments on cytogeography, phylogeny and chromosome morphology. Amer. J. Bot. 70: 1432–1443.

URBANSKA, K. M. 1983. *Antennaria carpatica* (Wahlb.) Bl. et Fing. s.l. in North America. I. Chromosome numbers, geographic distribution and ecology. Ber. Geobot. Inst. ETH Stiftung Rübel 50: 33–66.

DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF CALGARY
CALGARY, ALBERTA
CANADA T2N 1N4

RHODORA, Vol. 90, No. 862, 1988

SPIRANTHES NEBULORUM (ORCHIDACEAE), A NEW SPECIES FROM SOUTHERN MEXICO AND GUATEMALA

PAUL M. CATLING AND VIVIAN R. CATLING

ABSTRACT

A new species, *Spiranthes nebulorum* Catling & Catling, is described. It occurs in southern Mexico and Guatemala on open, grassy or rocky slopes and in bogs at elevations of 2000–3150 m. Comparisons with related species are provided along with a distribution map and a key to *Spiranthes sensu stricto* in southern Mexico and Guatemala.

Key Words: *Spiranthes*, new species, southern Mexico, Guatemala

The genus *Spiranthes* L. M. C. Richard (Mem. Mus. Paris 4: 50. 1818. *Nom. cons.*) is a member of the family Orchidaceae, subfamily Neottioideae. Approximately 415 binomials have been published in *Spiranthes,* but a restructuring of the genus by Garay (1980) suggests that *Spiranthes* in the strict sense includes approximately 40 species. Characters important in defining the genus in the strict sense include an anterior stigmatic surface below the terminal rostellum, a free dorsal sepal, an entire anther, a pollinarium with a cushion-type viscidium, a column that is not inflated and a rostellum that is divided into two sharply filiform segments (Garay,1980; Greenwood,1982).

Study of living material in southern Mexico and subsequent examination of specimens from 12 herbaria revealed the new species here described.

Spiranthes nebulorum Catling & Catling *sp. nov.* (Figure 1)

Herba terrestris erecta 18–33 cm alta, inferne glabra, superne trichomatibus capitatis septatis copiose obsita. Radices succulentae usque ad 3 mm diam. Folia 2–5 basalia linearia-lanceolata vel anguste oblonga-lanceolata usque ad 9 cm longa et 8 mm lata. Caulis usque ad 2 mm diam., bracteis 3–7, vaginantibus, 0.8–5 cm longis instructus. Spica densa, 3.5–9.5 cm longa, bracteis floriferis viridibus acuminatis 6–15 mm longis. Flores 10–30 in spiram densam contorti; perianthio horizontali, sepalis albis vel viridulis-albis ad basim nervis viridibus, petalis albis vel viridulis-albis, labello

albo vel viridulo-albo, sepalis lateralibus 5.5 7.5 mm longis, 1.7 2.8 mm latis, lanceolatis, acutis trinervibus, sepalo dorsali 5.4–7.5 mm longo, 3–4 mm lato, lanceolato, acuto, trinervi, petalis 6.5–7.8 mm longis, 1.5–2 mm latis, lanceolatis-falcatis uninervibus, labello 6.5–7.9 mm longo, 3–4.5 mm lato, subter laevi vel parvum verrucoso, prope basem latissimo, multo curvo, ungue 0.9–1.4 mm longo, cuneato, tuberculis ad basem prominentibus 1 1.8 mm longis, rostello elongato, emarginato.

Erect terrestrial herb, 18 33 cm tall, glabrous below, pubescent above with numerous septate, capitate trichomes. Roots fleshy, up to 3 mm in diameter. Leaves 2 5 basal, linear-lanceolate to narrowly oblong-lanceolate, up to 9 cm long and 8 mm wide. Stem to 2 mm thick, bearing 3 7 sheathing bracts 0.8 5.0 cm long. Spike densely spiralled, 3.5 9.5 cm long. Floral bracts green, acuminate, 6 15 mm long. Flowers 10 30; perianth horizontal; sepals white or greenish white with green nerves at the base, petals white or greenish-white, lip white or greenish-white. Lateral sepals 5.5 7.5 mm long, 1.7–2.8 mm wide, lanceolate, acute 3 nerved; dorsal sepal 5.4 7.5 mm long, 3 4 mm wide, lanceolate, acute, 3–nerved. Petals 6.5 7.8 mm long, 1.5 2 mm wide, lanceolate-falcate, 1 nerved. Lip 6.5 7.9 mm long, 3 4.5 mm wide, smooth below or obscurely verrucose, broadest near the base, arched, strongly curving upward from the claw, basal calli prominent, 1 1.8 mm long, the claw cuneate 0.9 1.4 mm long. Rostellum elongate, deeply emarginate.

TYPE. MÉXICO: Oaxaca: *ca.* 12 km N of Santa Maria Tlahuitoltepec, 3 km N of Santa Maria Yacochi along the road to Choapan, elev. 2500 m, 17° 11′ N, 96° 03′ W. UTM 814902, 7 September 1986, *P. M. Catling & V. R. Catling M28.5* (HOLOTYPE: AMO).

ADDITIONAL SPECIMENS EXAMINED. **México:** CHIAPAS: wooded slope in the Colonia 'Ach'lum, Municipio of Tenejapa, elev. 9100 ft., 23 Aug. 1966, *D. E. Breedlove 15262* (F, MICH); HIDALGO: 3 miles from Zacualtipán on road to Trianguistango, elev. 2000 m, 4 July 1947, *H. E. Moore Jr. 3323* (AMES); OAXACA: 18 miles SW of the city of Oaxaca, elev. 7500–9500 ft., 10–20 September 1894, *E. W. Nelson 1384* (AMES, US); Sierra de Clavellinas, elev. 9000 ft., 16–19 October 1894, *C. L. Smith 796* (MO, NY, US); Sierra de Clavellinas, elev. 9000 ft., 16 October 1894, *C. G. Pringle J 8 25* (AMES); at km 120 on road from Oaxaca to Tuxtepec, elev. 2120 m, 8 July 1979, *E. W. Greenwood G-885 & O. Suarez* (DAO); VERA CRUZ: Trinidad, 28 July 1904, *C. G. Pringle 11914* (AMES); Actopan, elev. 9000 ft., 12 Sept. 1938, *E. K. Balls B5554* (LA); El Huérfano, municipio de Chiconquiaco, elev. 2000 m, 10 July 1973, *F. Ventura A. 8584* (ENCB); 11 miles northwest of Jalapa, 1 Aug. 1960, *F. W. Gould 9259* (MICH). **Guatemala:** ALTA VERAPAZ: Coban, 1908, *H. von Türckheim 1832* (US); Coban, 1908, *H. von Türckheim 2334* (US); CHIMALTENANGO: Chichavac, elev. 2400 2700 m, 7 July 1933, *A. F. Skutch 362* (AMES, US); HUEHUETENANGO:

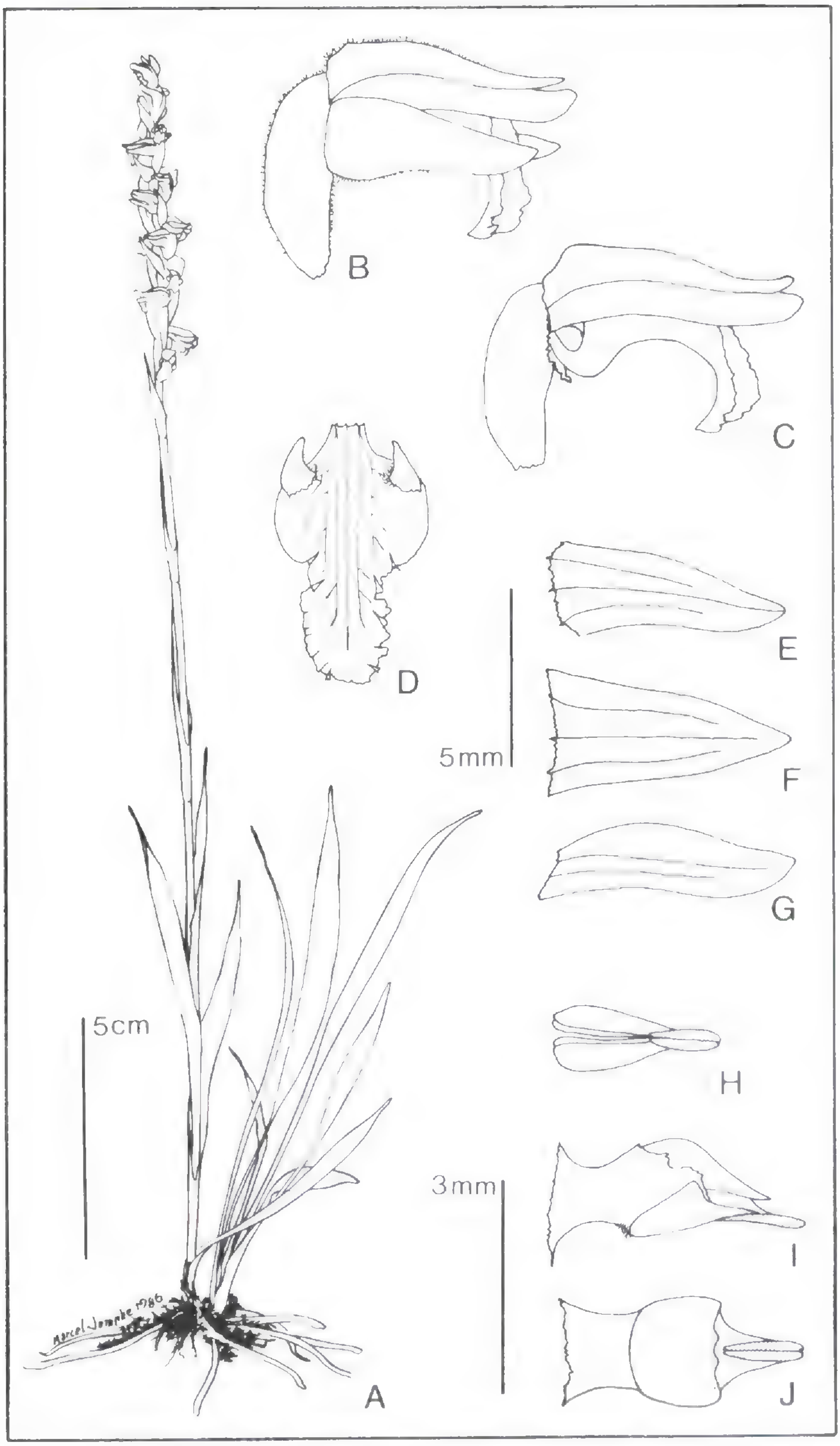


Figure 1. Drawing based on the holotype of *Spiranthes nebulorum* Catling & Catling (*Catling & Catling M28.5*, AMO). **A,** plant habit. **B-J,** camera lucida drawings of floral parts. **B,** lateral aspect of flower; **C,** lateral aspect of flower with lateral sepal removed; **D,** lip (flattened); **E,** lateral sepal; **F,** dorsal sepal; **G,** petal; **H,** pollinia; **I,** column, lateral aspect; **J,** column, ventral aspect.

Cerro Cananá, between Nucapuxlac and Cananá, Sierra de los Cuchumatanes, elev. 2500–2800 m, 18 July 1942, *J. A. Steyermark 49000* (AMES, F); along creek below Nucá and Quetzal, elev. 2100–2500 m, 30 July 1942, *J. A. Steyermark 49780* (F); top of Cerro Chemalito, Sierra de los Cuchumatanes, 3.5 miles W of Santa Eulalia, elev. 3100–3150 m, 2 Aug. 1942, *J. A. Steyermark 49920* (AMES, F).

A photograph of *Spiranthes nebulorum* accompanied the recent synopsis of Mexican Spiranthinae by Burns-Balogh (1986, Figure 10, *sub S. graminea, G-885*).

Spiranthes nebulorum occurs on open grassy and rocky slopes, and in sphagnum bogs at elevations of 2000–3150 m. Its distribution includes the southern Sierra Madre Oriental of Mexico, the mountains in the Mexican states of Oaxaca and Chiapas, and the Guatemalan departments of Alta Verapaz, Chimaltenango, and Huehuetenango (Figure 2). The specific epithet refers to the frequently foggy conditions at the elevations where it is found.

The early collections of *Spiranthes nebulorum* were identified as *S. graminea* Lindley. Judging by his annotations on specimens at AMES in 1940, Correll recognized that some of the plants previously determined as *S. graminea* from Mexico and Guatemala had an ovate instead of oblong-quadrate lip. He referred these plants (i.e., those described here as *S. nebulorum*) to *S. vernalis* Engelm. & Gray, and they were reported as such by Ames & Correll (1952) and later by Williams (1965). *Spiranthes vernalis* differs from *S. nebulorum* in its much narrower sepals, non-diverging lateral veins in the lip (Figure 3), and dense, hispid and pointed pubescence in the inflorescence.

Spiranthes nebulorum has capitate hairs on the inflorescence like *S. graminea*, but differs from the latter species by its more basally curved and longer-clawed lip (Figures 1 & 4), that is less obviously verrucose below. In addition, the lip of *S. nebulorum* is usually wider in the basal half than in the distal half, less dark and fleshy, less crisped distally, and has more prominent basal calli 1–1.8 mm instead of 0.4–0.8 mm long. The lateral sepals of *S. nebulorum* are wider, being 1.7–2.8 mm wide instead of 1.2–1.8 mm wide, and the flowers are wider with a wide separation between the lateral and dorsal sepals. *Spiranthes graminea* has a different distribution, occurring mainly in the Sierra Madre Occidental and the mountains of the central Mexican plateau. It does not extend to Guatemala or the state of Chiapas.

Spiranthes nebulorum is apparently related to *S. laciniata* (Small) Ames and *S. praecox* (Walt.) S. Wats., both of eastern North America. Such a pattern of relationship is well documented for the flora

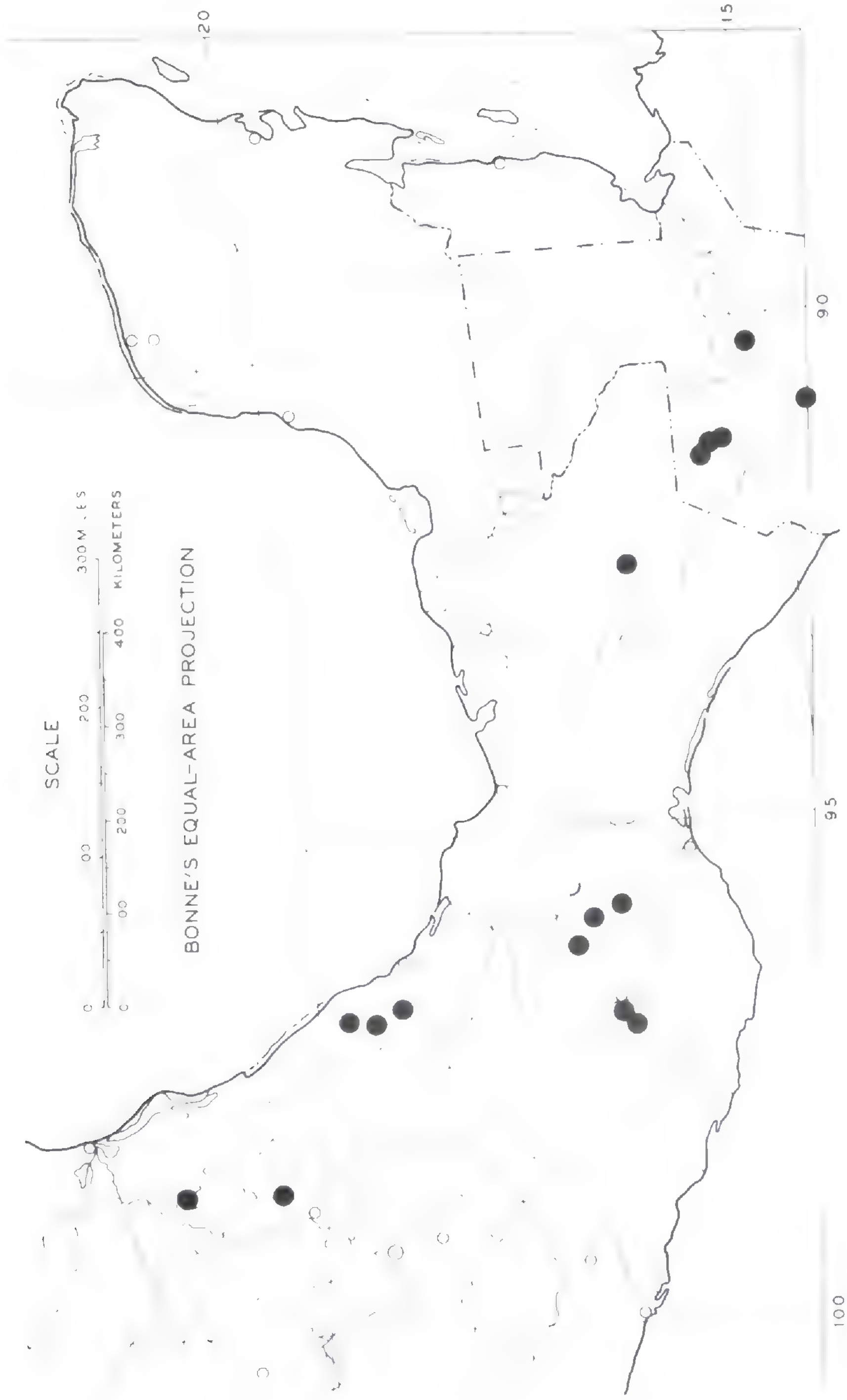


Figure 2. Map of central Mexico and northern Guatemala showing the distribution of *Spiranthes nebulorum* (dots). Open circles indicate major cities. Political boundaries are indicated by lines of dashes and dots.

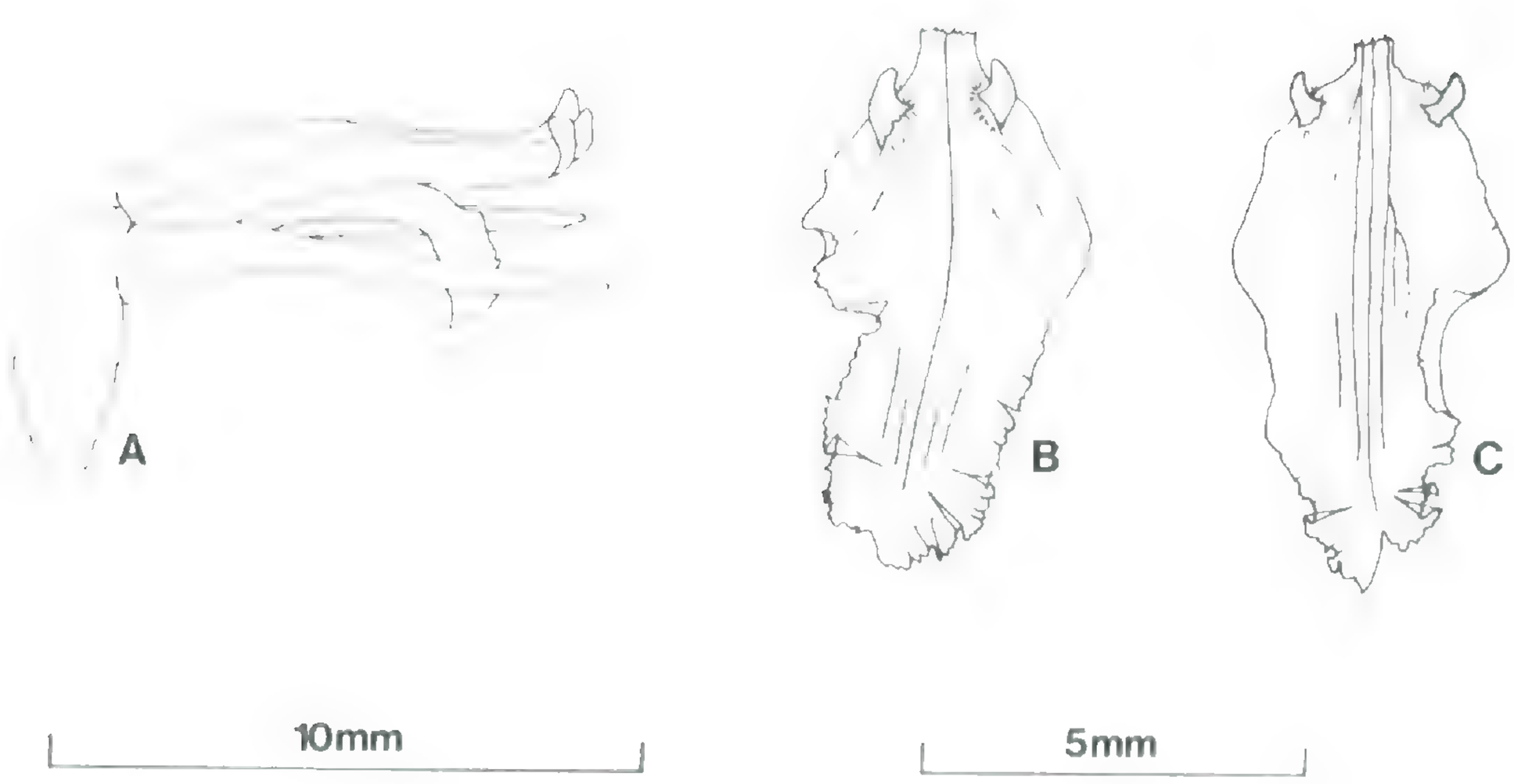


Figure 3. Camera lucida drawings of a flower from the holotype of *Spiranthes vernalis* Engelmann & Gray (*Lindheimer 189, 191*, AMES). **A**, lateral aspect of flower; **B,C**, lips (flattened).

of the eastern Mexican highlands (Miranda & Sharp, 1950). *Spiranthes praecox* is similar to *S. nebulorum* in having a lip that is membranous, smooth below, and with the primary veins thickened and diverging near the tips. *Spiranthes praecox* differs, however, in being a larger plant, 30–60 cm tall, with somewhat longer and much narrower, white flowers. The dorsal sepals of *S. praecox* rarely exceed 2.3 mm in width, whereas in *S. nebulorum* they range from 3–4 mm in width. The lip of *S. praecox* is oblong instead of lanceolate, less prominently arched basally, and with shorter calli 0.5–1.2 mm long. Finally, *S. praecox* has a narrower column with the stigmatic surface as long as or longer than wide. In *S. nebulorum* the column is relatively wide and the stigmatic surface is clearly wider than long.

Spiranthes nebulorum resembles *S. laciniata* in its relatively wide flowers and lip that is prominently arched basally and has a relatively long claw and relatively long calli. *Spiranthes laciniata* is a larger plant (20–100 cm tall) with larger flowers (6–9 mm long), differing from *S. nebulorum* in its more loosely spiralled inflorescence of white flowers, each with a very thick and fleshy, yellowish lip. In *S. laciniata* the lateral venation near the apex of the lip is parallel, and the lip is prominently verrucose below, while in *S. nebulorum* the terminal lateral venation is divergent and the lip is obscurely verrucose below.

Spiranthes nebulorum also resembles *S. ochroleuca* (Rydb.) Rydb. and *S. casei* Catling & Cruise, both plants of northeastern

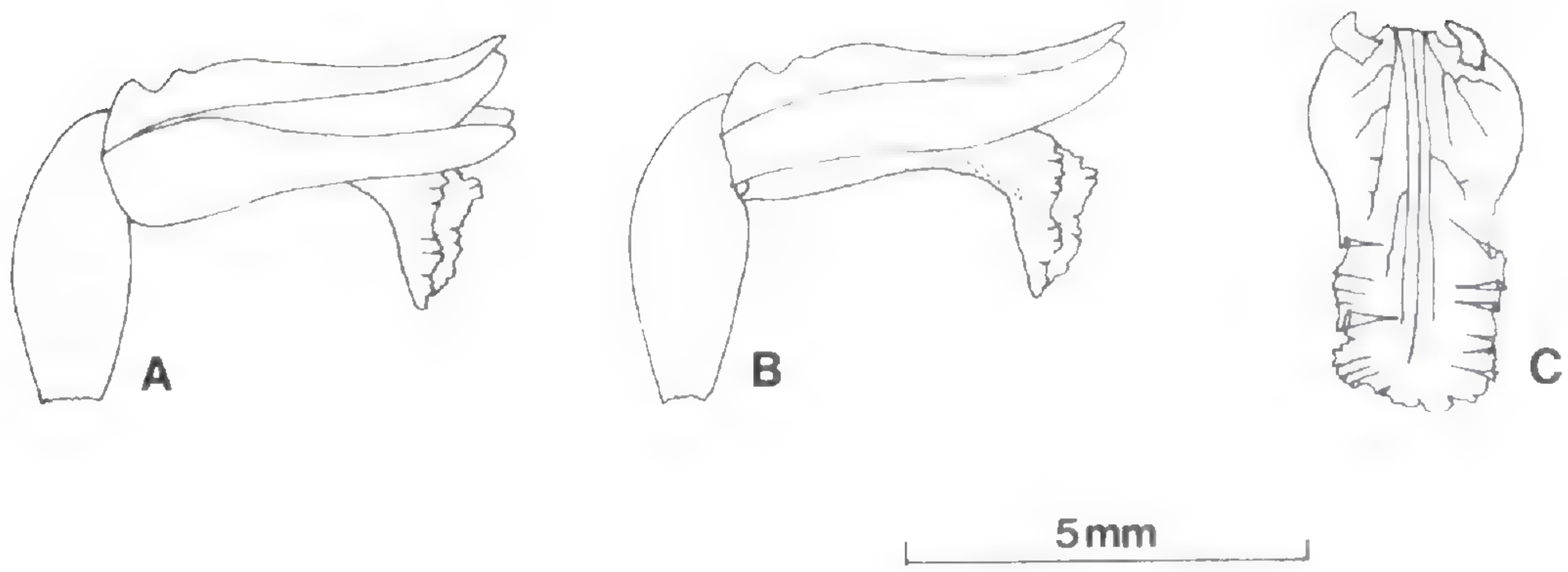


Figure 4. Camera lucida drawings of a flower from the holotype of *Spiranthes graminea* Lindley (*Hartweg 224*, K). **A,** lateral aspect of flower; **B,** lateral aspect of flower with lateral sepals removed; **C,** lip (flattened).

North America. It differs from both of these species in its narrow linear leaves and in the terminally thickened and diverging veins of the lip.

The following key separates *S. nebulorum* from other *Spiranthes sensu stricto* currently recognized in southern Mexico and Guatemala. Statements regarding floral dimensions (including those in the description and key) exclude flowers from the very top of the inflorescence (upper 1/5). Flowers from this position are often reduced in size. Interspecific differences have been shown to be most evident in the lower flowers of the *Spiranthes* inflorescence (Catling, P. M. 1980. Systematics of *Spiranthes* L. M. C. Richard in northeastern North America. Ph. D. thesis, Univ. of Toronto).

KEY TO *SPIRANTHES* IN SOUTHERN MEXICO AND GUATEMALA

1. Pubescence of the inflorescence axis dense, hairs mostly stiffly erect, 3 5 septate, tapering toward apex, often appearing clearly pointed ..... *S. vernalis* Engelm. & Gray (and an apparently closely related agamospermic or autogamous taxon from Oaxaca (*Greenwood 1126* AMO) that is very rare)

1. Pubescence of the inflorescence axis sparse and short or dense and flexuous, 2 11 septate, hairs distinctly expanded and glandular at the apex or equally wide throughout their length 2

2. Pubescence of the inflorescence axis sparse and short, longer hairs 0.1–0.23 mm long, 2 -3 septate; flowers loosely spiralled, white with green in the central portion of the lip; lateral sepals 4–6 mm long ..... *S. torta* (Thunb.) Garay & Sweet (including *S. amesiana* Schltr.)

2. Pubescence of the inflorescence axis relatively thick and long, longer hairs 0.4–0.6 mm long, 8–11 septate; flowers densely spiralled (sometimes to the extent of appearing as 3 spiralling ranks), greenish-white or creamy-white, centre of the lip pale yellowish or creamy; lateral sepals 5–7 mm long 3

3. Lip broadly ovate, strongly curving upward from the claw and consequently the floral tube arched and widened basally (Figure 1); basal calli 0.9–1.8 mm long; lateral sepals 1.7–2.8 mm wide .....
..... *S. nebulorum* Catling & Catling

3. Lip oblong-ovate or oblong-quadrate, not strongly curving from the claw and floral tube straight and not widened basally (Figure 4); basal calli 0.4–0.8 mm long; lateral sepals 1.2–1.8 mm wide .....*S. graminea* Lindley

ACKNOWLEDGMENTS

Leslie A. Garay (AMES) kindly assisted with the examination of material. Charles J. Sheviak (NYS), Edward W. Greenwood (AMO) and Eric A. Christenson (SEL) provided useful comments on the manuscript. Permission to dissect flowers from type material at their collections was kindly granted by Leslie A. Garay (AMES) and Peter Taylor (K). Marcel Jomphe (DAO) kindly assisted in preparing the illustration of the new species.

LITERATURE CITED

Ames, O. and D. S. Correll. 1952. Orchids of Guatemala. Fieldiana, Bot. 26(1): I-XIII.

Burns-Balogh, P. 1986. A synopsis of Mexican Spiranthinae. Orquidea (Méx.). 10: 47-96.

Garay, L. A. 1980. A generic revision of the Spiranthinae. Bot. Mus. Leafl. 28: 277–425.

Greenwood, E. W. 1982. Viscidium types in the Spiranthinae. Orquidea (Méx.). 8: 303–310.

Miranda, F. and A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31: 313–333.

Williams, L. O. 1965. The Orchidaceae of Mexico. Escuela Agricola Panamericana, Tegucigalpa, Honduras.

P. M. C.
BIOSYSTEMATICS RESEARCH CENTRE
AGRICULTURE CANADA
WM. SAUNDERS BLDG.
CENTRAL EXPERIMENTAL FARM
OTTAWA, ONTARIO
CANADA K1A 0C6

V. R. C.
8 SCRIVENS DRIVE, R.R. 3
METCALFE, ONTARIO
CANADA K0A 2P0

RHODORA, Vol. 90, No. 862, 1988

A FIRST REPORT FOR *CAREX HYPSIPEDOS* (CYPERACEAE) IN ARGENTINA AND BOLIVIA AND THE STATUS OF *C. PHALAROIDES* VAR. *PARVULA* IN SOUTHERN SOUTH AMERICA

GERALD A. WHEELER

ABSTRACT

Carex hypsipedos C. B. Clarke (Cyperaceae) is reported for the first time in Argentina and Bolivia, where it grows in alpine meadows. *Carex phalaroides* Kunth var. *parvula* Rud. Gross, which was described from northwestern Argentina, is here considered to be conspecific with *C. hypsipedos*.

Key Words: *Carex hypsipedos,* taxonomy, synonymy, new record, Argentina, Bolivia

While *Carex hypsipedos* C. B. Clarke has been previously reported from Peru (Clarke, 1906; Kükenthal, 1909 [as *C. umbellata* Schk. ex Willd. var. *depressa Kü*k.]; Macbride, 1936), this note represents the first report of it from Argentina and Bolivia. Examination of the holotype specimen of *C. phalaroides* Kunth var. *parvula* Rud. Gross reveals it to be conspecific with *C. hypsipedos*. Full citations for specimens mentioned below are given near the end of this report.

Carex hypsipedos was described by Clarke in 1906 from plants collected (*Weberbauer 2617*) in the department of Junín, Peru. This name was not accounted for by Kükenthal (1909), who treated Weberbauer's plants as *Carex umbellata* var. *depressa*. Although *C. hypsipedos* belongs in sect. *Montanae*, it differs considerably from the North American *C. umbellata,* a conclusion also arrived at by Macbride (1936). In *C. hypsipedos* the perigynia are few to several veined and the culms are all quite short. By contrast, in *C. umbellata* the perigynia have 2 prominent veins (the rest obscure) and the culms are of various lengths, some spikes on moderate to long peduncles and others on much shorter ones. It is noteworthy that *C. hypsipedos* is the only member of sect. *Montanae* thus far reported from South America.

In 1941 Gross described *Carex phalaroides* var. *parvula* from plants collected (*Venturi 6491*) in Jujuy Province, Argentina. Barros (1947) did not treat this taxon (at any rank) in his comprehensive treatment of the Cyperaceae of Argentina.

Table 1. Characters used to differentiate *Carex hypsipedos, C. brachycalama,* and *C. phalaroides.*

Character	Venturi 6491	*C. hypsipedos**	*C. brachycalama***	*C. phalaroides****
Achenes				
outline	obscurely 3-angled	obscurely 3-angled	obscurely 3-angled	sharply 3-angled
sides	convex	convex	convex	flat or concave
Perigynia				
body	slightly pubescent, membranous	slightly pubescent, membranous	glabrous, subcoriaceous	pubescent, membranous
beak	scaberulent	scaberulent	smooth	scaberulent
Pistillate scales				
shape	lanceolate	lanceolate	broadly ovate	ovate
apex	acuminate or short-awned	acuminate or short-awned	cuspidate or mucronate	with long, rough awns
length	2.8–4.2 mm long	2.6–4.3 mm long	2–2.6 mm long	3–4 mm long (excluding awn)
color	reddish-brown	reddish-brown	chestnut or stramineous	greenish
Terminal spike				
gender	entirely staminate	entirely staminate	entirely staminate	androgynous
peduncle	minutely scabrous	minutely scabrous	smooth	minutely scabrous
Culms	cespitose	cespitose	solitary or few together	loosely cespitose
Basal sheaths	reddish-tinged	reddish-tinged	pale brown	pale brown

*Data from Clarke (1906), Kükenthal (1909), Macbride (1936), and photograph and fragment of *Weberbauer 2617* [F].

**Data from Grisebach (1879), Kükenthal (1909), Macbride (1936), and *Hieronymus 759* (*see* Representative Specimens).

***Data from Kükenthal (1909) and *Sellow s.n.* [isotype: K!].

After a thorough and careful examination of the Venturi specimen, it is abundantly clear that the specimen is not closely related to *Carex phalaroides* (Table 1) and, in fact, is an anomaly in *Carex* sect. *Digitatae,* the section in which *C. phalaroides* and its varieties are generally placed (e.g., Kükenthal, 1909). The achenes of the Venturi specimen are obscurely 3-angled and have convex sides (at

least above), unlike members of sect. *Digitatae* which have sharply 3-angled achenes with flat or concave sides. The morphology of the Venturi specimen indicates placement in sect. *Montanae*, and indeed the morphological features appear identical with those of *C. hypsipedos* (Table 1).

Besides the Venturi specimen, two other specimens (*Castillon 6642* and *Ruthsatz 376/2*) from Jujuy Province, Argentina, are assignable to *Carex hypsipedos*. Both specimens were originally identified as *C. brachycalama* Griseb., a member of sect. *Paniceae* (Kükenthal, 1909). While *C. hypsipedos* and *C. brachycalama* closely resemble each other in habit (Macbride, 1936), the two species are differentiated by a number of morphological features, the most salient of which are given in Table 1. Both *C. hypsipedos* and *C. brachycalama* occur in South America (Fig. 1), and the latter species also has been reported from Mexico (González, 1983). Although *C. hypsipedos* is apparently sympatric with *C. brachycalama* in South America and may be confused with it, the two species, as indicated above, are easily separated by certain characters (Table 1).

Barros (1947) reported *Carex brachycalama* from Córdoba and Jujuy provinces in Argentina. While *C. brachycalama* occurs in Córdoba Province (the type, *Hieronymus 759*, was collected in the Sierra de Achala about 75 km SW of the city of Córdoba), no specimen has been seen to support its presence in Jujuy Province. Barros's (1947) report of *C. brachycalama* from Jujuy Province was based on a specimen (*Castillon 6642*) assignable, as indicated above, to *C. hypsipedos*.

Because not all of the morphological variation displayed by *Carex hypsipedos* is reflected in previous descriptions, a more complete description is given below; complete synonymy for *C. hypsipedos* is also provided here.

Carex hypsipedos C. B. Clarke, in Urban, Bot. Jahrb. Syst. 37: 518. 1906. TYPE: PERU: Dpto. Junín, La Oroya, in pratis alpinis 4300 m, [1903,] *Weberbauer 2617* (HOLOTYPE: ? USM; ISOTYPE: F-607385, photograph! and fragment! from B [specimen at B destroyed]).

Carex umbellata Schk. ex Willd. var. *depressa* Kük., in A. Engler, Das Pflanzenreich, IV. 20, Heft 38: 453. 1909. TYPE. *Weberbauer 2617* (HOLOTYPE: B [destroyed]). [To my knowledge, the fragment of *Weberbauer 2617* at F (see above) is the only remaining material of the plants used by Kükenthal (1909) in describing *C. umbellata* var. *depressa*.]

Carex phalaroides Kunth. var. *parvula* Rud. Gross, Repert. Spec. Nov. Regni Veg. 50: 211. 1941. TYPE. ARGENTINA: Prov. Jujuy, [Dpto. Tilcara,] Titeara [sic], 2500

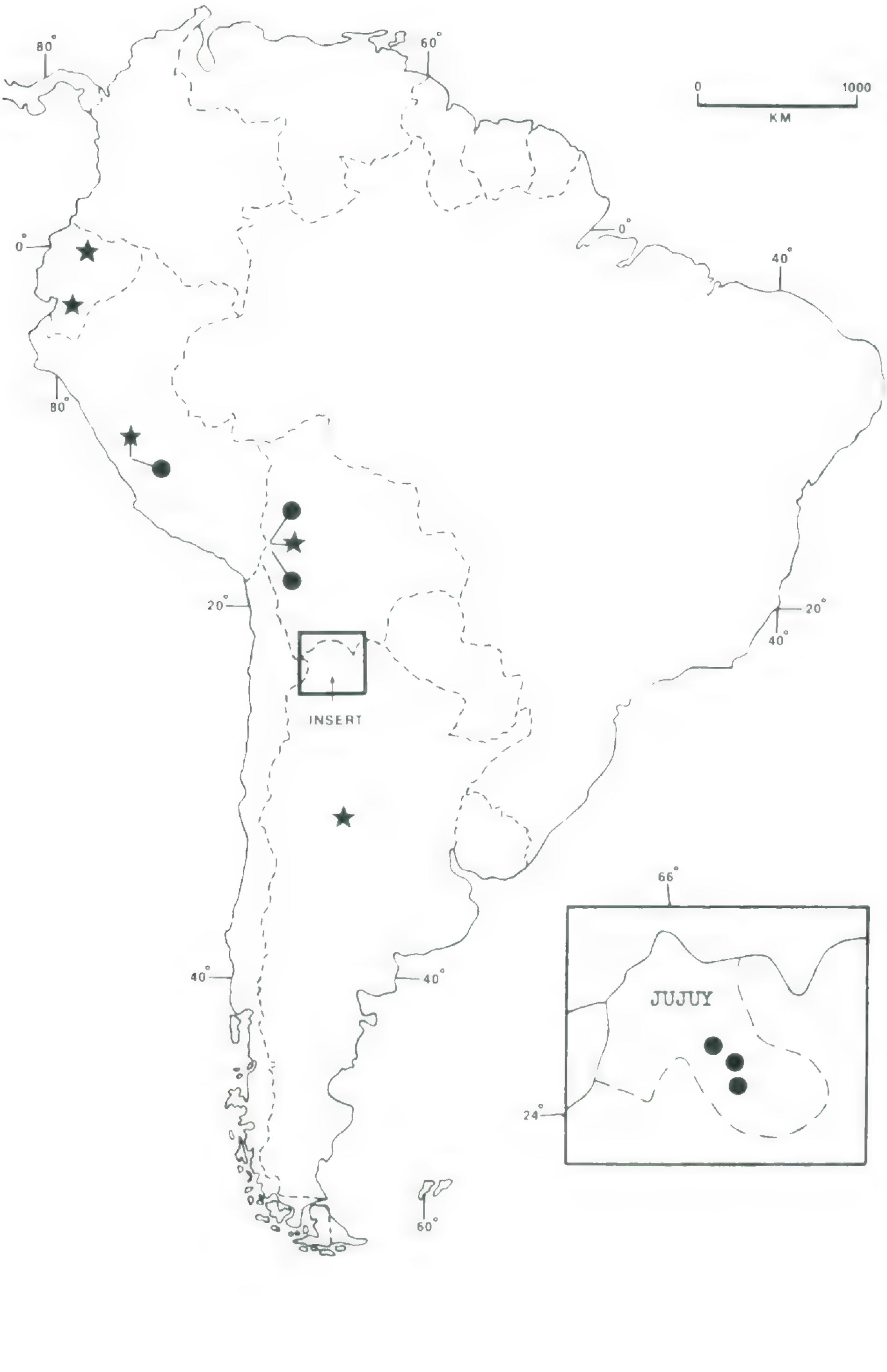


Figure 1. Map of South America showing distributions of *Carex hypsipedos* (dots) and *C. brachycalama* (stars). Stations for *Carex brachycalama* in Mexico are not shown.

m, [15 Feb 1927,] *Venturi 6491* (HOLOTYPE: US-1545831!). [The correct spelling for the locality where the holotype was collected is Tilcara.]

Plants low-growing, cespitose; fertile culms 1–4 cm tall, erect, with reddish-tinged basal sheaths, these more or less fibrillose. Leaves of flowering shoots 3–7, erect or slightly curved, mostly exceeding culms; blades 10–55 mm long, 0.8–2.5 mm wide, flat, margins smooth or scabrous (especially distally); leaf sheaths glabrous, pale brown; inner band of sheaths pale brown or hyaline, glabrous, apex concave; ligules short (less than 2 mm long), rounded, slightly wider than long. Vegetative shoots 2.5–7 cm tall; leaves 5–11, similar to those of fertile culms; pseudoculms 1–2 cm tall. Inflorescences (10–)15–30 mm long, the lateral spikes approximate or overlapping; spikes erect on short peduncles; peduncles slender but stiff, 0.5–12 mm long, slightly scabrous (rarely smooth). Spikes 3–4, the terminal staminate (very rarely with 1 or 2 perigynia at base of spike), the lateral pistillate. Terminal spikes 6.5–8 mm long, 2–3.5 mm wide, subtended by a sheathless bract; bracts slightly shorter to longer than the terminal spike, body 4–5 mm long, 1.6–1.8 mm wide, 3–5-veined, with a scabrous awn 0.5–7 mm long. Lateral spikes 4–6.5 mm long, 2.8–5 mm wide, 3–8-flowered. Pistillate scales 2.6–4.3 mm long, 1.3–1.7 mm wide, lanceolate, acuminate, midvein sometimes excurrent as a short awn, about equal to or slightly longer and wider than the perigynia (but not concealing them), reddish brown or hyaline, with greenish center, 5-veined. Staminate scales 3.5–5 mm long, 1.2–1.6 mm wide, lanceolate to narrowly oblong, acuminate, glabrous, but sometimes sparingly scaberulent on the veins distally, reddish brown, with narrow hyaline margins and stramineous center, 3–5-veined. Perigynia 2.4–3.2 mm long, 1.2–1.6 mm wide, the body oblong-obovoid or elliptical, short-pubescent to glabrate, 2 veins prominent and the rest (6–10 veins) faint or distinct, membranaceous, dull green or greenish-brown or stramineous and sometimes reddish-tinged near the beak, stipitate, abruptly contracted to a beak; beaks 0.4–0.6 mm long, scaberulent, shallowly bidentate, teeth about 0.2 mm long. Achenes 1.8–2.2 mm long, 1.1–1.5 mm wide, oblong-obovoid, with blunt angles, the sides convex (at least above), tapering at base, short-apiculate, yellowish brown, very closely enveloped by the perigynium. Style jointed with achene; stigmas 3. Anthers 3, ca. 1.5 mm long.

Carex hypsipedos is a rarely collected species that in both Argentina and Bolivia is a low-growing, alpine plant whose fertile culms seldom reach 4 cm in height. The plants occur from about 2500 to

4500 m and bear fruit in January and February. In Peru (Macbride, 1936), *C. hypsipedos* also occurs as a depressed, alpine species that primarily grows in páramos above 4000 m. Although both *Carex hypsipedos* and *C. brachycalama* grow in alpine meadows, the former species seemingly grows in drier sites than the latter.

Carex hypsipedos

REPRESENTATIVE SPECIMENS: **Argentina.** Prov. Jujuy: Estación Volcán, Mula Muerta, 3200 m, pradera alpestre, 7 Jan 1919, *Castillon 6642* (LIL-9873); Dpto. Humahuaca, Mina El Aguilar, 4450 m, 21 Feb 1972, *Ruthsatz 376/2* (NY). **Bolivia.** Dpto. La Paz, Prov. Manco Kapac: Isla del Sol, Cerro Chequesani, 4020 m, 21 Jan 1986, *Liberman 1094* (MICH); Sur Challa, 3840 m, 25 Jan 1986, *Liberman 1246* (MICH).

Carex brachycalama

REPRESENTATIVE SPECIMENS: **Argentina.** Prov. Córdoba: Sierra de Achala, Río del Catre, 4 Feb 1877, *Hieronymus 759* (isotypes: F-51053!, P!, F-723581 [photograph! of B; specimen at B destroyed]. **Bolivia.** Dpto. La Paz: Prov. Manco Kapac, Isla del Sol, 3820 m, 24 Jan 1986, *Liberman 1211* (MICH). **Ecuador.** Prov. Azuay: vicinity of Toreador, between Molleturo and Quinoas, 3810–3930 m, 15 June 1943, *Steyermark 53227* (F-1266187) and *53157A* (MO); Cerro Antisana, 0°30′S, 78°00′W, Hacienda Antisana, 4110 m, 4 Aug 1960, *Grubb 673* et al. (partim K). **Peru.** Dpto. Junín: vicinity of Chinche, hacienda 9 mi. up river from Yanahuanca, ca. 11500 ft, 21 June 1922, *Macbride & Featherstone 1274* (F-517784).

ACKNOWLEDGMENTS

The writer thanks Dr. Anton A. Reznicek for information on *Carex brachycalama* in Mexico and Bolivia and for permitting me to examine specimens of *C. hypsipedos* from Bolivia that are at MICH. The author also thanks the directors and curators of the other herbaria whose specimens were utilized in the study: F, K, LIL, MO, NY, P, and US.

LITERATURE CITED

BARROS, M. 1947. Cyperaceae: Scirpoideae, Rhynchosporoideae, Caricoideae. *In:* H. R. Descole. Genera et Species Plantarum Argentinarum. Tomus IV (II). pp. 259–539.

CLARKE, C. B. 1906. *Carex*. *In:* I. Urban. Plantae novae andinae imprimis Weberbauerianae. II. Bot. Jahrb. Syst. 37: 518–519.

GONZÁLEZ, S. 1983. Nuevos registros de ciperáceas para la flora del valle de Mexico y de la Republica Mexicana. Bol. Soc. Bot. México 44: 17–21.

GRISEBACH, A. 1879. Symbolae ad floram argentinam. Abh. Königl. Ges. Wiss. Göttingen 24: 310–316.

GROSS, R. 1941. Cyperaceae novae austro-americanae. Repert. Spec. Nov. Regni Veg. 50: 210–213.

KÜKENTHAL, G. 1909. Cyperaceae: Caricoideae. *In:* A. Engler, Ed. Das Pflanzenreich 38 Heft (IV. 20): 1–824. Leipzig: Wilhelm Engelmann.

MACBRIDE, J. F. 1936. *Carex* in Flora of Peru. Field Mus. Nat. Hist., Bot. Ser. 13: 314–320.

DEPARTMENT OF BOTANY
220 BIOLOGICAL SCIENCES CENTER
UNIVERSITY OF MINNESOTA
ST. PAUL, MINNESOTA 55108

RHODORA, Vol. 90, No. 862, 1988

THE CORRECT NAME FOR ELLIOTT'S GOLDENROD

LEONARD J. UTTAL AND DUNCAN M. PORTER

ABSTRACT

Solidago latissimifolia Miller, herein lectotypified, is an older name for the plants currently known as *S. elliottii* Torrey & Gray and *S. elliptica* Aiton. Nomenclatural histories of the species are analyzed, and leaf characters of several similar goldenrod species are compared. Lectotypification of *S. latifolia* Linnaeus and the current custom of tracing European *Solidago* cultivars to American indigenous ancestry are discussed. *Solidago aestivalis* Bicknell replaces *S. rugosa* var. *sphagnophila* Graves. Endangerment prospects of *S. latissimifolia* are presented.

Key Words: *Solidago*, Elliott's Goldenrod, goldenrod, lectotypification, nomenclature, endangerment, eastern U.S. coast

INTRODUCTION

In studying *Solidago flaccidifolia* Small, a species with axillary clusters of heads that occurs from Virginia to Florida and Oklahoma, Uttal noted that, according to Cronquist (1980), Small (1933) misapplied the name *S. latissimifolia* Miller (1768) to the species. We agreed, and felt we should examine the proper application of *S. latissimifolia*. A search of the literature was begun, and we requested photographs and analyses of pertinent specimens in the British Museum (Natural History). These were very kindly supplied by Mr. A. O. Chater.

It became evident that Miller's description of *Solidago latissimifolia* applies to what has been passing as *S. elliottii* Torrey & Gray, a showy species of damp sandy soils of the outer Atlantic Coastal Plain from Nova Scotia and Massachusetts to Florida. It has tight to open pyramidal panicles with the capitula mostly secund ("secund-paniculate"). The plants are glabrous throughout except for slight puberulence in the inflorescence. The leaves are non-triplinerved, smooth, subcoriaceous, closely to remotely simply-serrate with the teeth callus-tipped; the margins are subrevolute, cartilaginous, and closely ciliolate. Rarely, the veins of the undersurface bear a few setae; usually the leaves are completely glabrous above and beneath.

The leaves of the other non-triplinerved species of eastern North American secund-paniculate goldenrods differ from those of *Solidago elliottii* (sensu *S. latissimifolia* Miller) as follows:

1. *S. aestivalis* Bicknell — leaves rugose, doubly serrate.
2. *S. fistulosa* Miller — leaves clasping, pubescent at least on upper surfaces.
3. *S. gattingeri* Chapman — leaves strongly ciliate.
4. *S. patula* Muhlenberg — leaves scabrous on upper surfaces.
5. *S. rugosa* Miller - leaves rugose, pubescent (the glabrous *S. rugosa* var. *sphagnophila* Graves is here synonymized with *S. aestivalis*).
6. *S. uliginosa* Nuttall — petioles clasping.
7. *S. ulmifolia* Muhlenberg — leaves pubescent on lower surfaces.

At our request, A. O. Chater located Miller's specimen of *Solidago latissimifolia*, originally cultivated at the Jardin du Roi, Paris, in BM (Figure 1). It is quite like indigenous plants of *S. elliottii* from Massachusetts and Nova Scotia, but deviates from them in that the upper part of the inflorescence axis is crooked and many of its lateral branches are aborted, as if from insect damage. Similar plants occur in native populations (Figure 2). It is interesting that Miller (1768) gave the locality for his plant as "Canada"; many plants from Nova Scotia have the "white stalk" (epidermis) he refers to in his description. In 1753, Linnaeus, in describing *Solidago latifolia*, cited a figure in Plukenet's 1694 *Almagestum* (t. 235, f. 4). Gray (1882) deduced, and Porter later verified, that the specimen used for Plukenet's (1694) engraving is *Solidago latissimifolia*. The engraving is somewhat stylized, and the specimen has more leaves and tighter racemes than illustrated. By separating this discordant element from *S. latifolia* L., Gray (1882) effectively lectotypified the descriptive element of the Linnaean *S. latifolia*. Mackenzie (1928) made *S. latifolia* L. a synonym of *S. flexicaulis* L.

Our selection of the lectotype for *Solidago latissimifolia* was reinforced by an appropriate annotation by Solander (copied in the hand of Dryander). The sheet is also annotated by Solander that the specimen is the *S. elliptica* of Aiton's *Hortus Kewensis* (1789) (Figure 1).

Approximately 500 herbarium specimens of *Solidago elliottii* were examined in this study, and field observations of the species were made in Virginia and South Carolina. Wide variation in panicle development was noted. In some specimens (Figures 3, 4), the upper racemes are non-secund, but even so there is always some secundity in the lower racemes.

It appears that replacement of the name *S. elliottii* by *Solidago latissimifolia* is mandated by the principle of priority. However, shortly after the description of *S. latissimifolia* was published, the species embarked upon what is now a tortuous nomenclatural history.

Aiton (1789) described *Solidago elliptica* based on two specimens annotated by Solander (Figures 1, 3). The paralectotype (*see* Porter, 1987) (Figure 3) appears markedly different from the lectotype (Figure 1), having a wide diffuse panicle, with the upper racemes non-secund and the lower secund. It was annotated as conspecific with the lectotype by Solander before his death in 1782. In 1841, Gray (Torrey & Gray, 1841) took the paralectotype specimen to be the type of *S. elliptica* Aiton, and despite the priority of *S. latissimifolia*, he assigned Miller's 1768 species to synonymy of *S. elliptica*. Gray used the name *S. elliptica* for the indigenous plants of the salt marshes of New York, a phase of the species nowadays found from Long Island to southern New Jersey (Figure 4). Miller's Kew specimen probably originated from material gathered in this area. Later, Gray (1882) described the lectotype specimen of *Solidago latissimifolia* which he had seen earlier at the British Museum as *S. elliptica* var. *axilliflora*, a cultivar popular in Europe, and one he deemed not traceable to indigenous ancestry in the U.S. The "typical" variety of *S. elliptica* he reduced to synonymy, calling it a large form of *S. elliottii*. Four years later, Gray (1886) changed his mind and treated *S. elliptica* as another European cultivar not traceable to indigenous U.S. ancestry. Thereafter, botanists ceased using the name *S. elliptica* for American plants, referring to all such specimens as *S. elliottii*.

Now, let us trace the origin of the name *Solidago elliottii* Torrey & Gray. Elliott (1824) doubtfully assigned a plant he collected on Parris Island, South Carolina to *S. elliptica* Aiton. Elliott seems to have known of the relationships of *S. elliptica* to *S. latissimifolia*, for he said that his plant agreed with *S. elliptica* in many respects, "but I have seen no leaves that would merit Miller's epithet of Latissimifolia." We doubt that Elliott saw specimens of his species from any northern station. The leaves of *S. latissimifolia* in several collections from Beaufort, South Carolina, about eight km from Elliott's station, are wider and shorter than from plants collected further north, but are otherwise in accord with the Miller (1768) description "*foliis nervosis serratis glabris*," as are the heads and panicles.

Figure 1. Lectotype of *Solidago latissimifolia*; from the Jardin du Roi, Paris, early 18th century.

Figure 2. Indigenous plant of *Solidago latissimifolia* from Massachusetts.

Figure 3. Paralectotype of *Solidago elliptica;* from Kew, 1778 = *S. latissimifolia*.

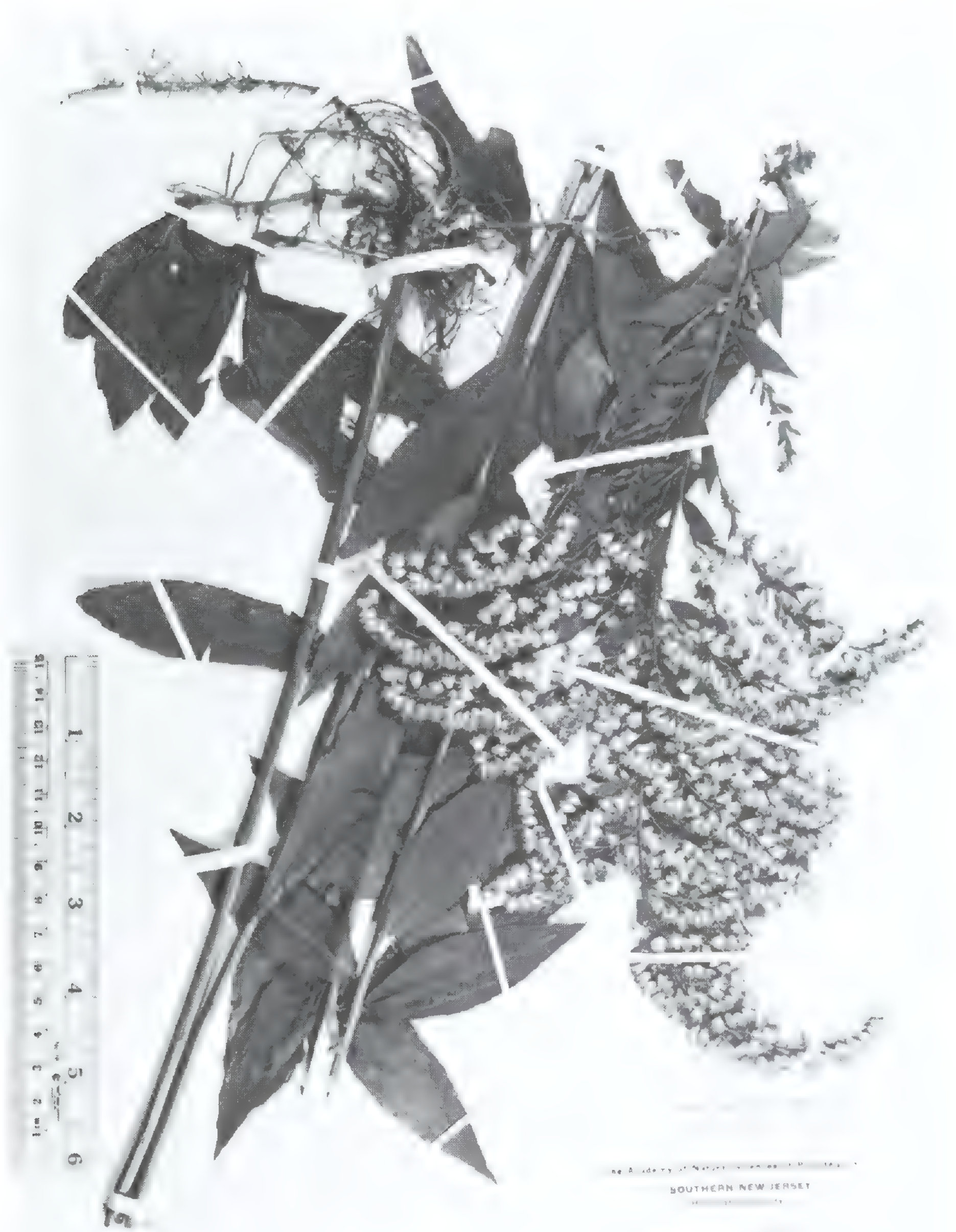


Figure 4. Indigenous plant of *Solidago latissimifolia,* open-panicled phase, from New Jersey.

Gray (Torrey and Gray, 1841) considered Elliott's collection of *Solidago elliptica* to represent a new species, *Solidago elliottii* Torrey & Gray. With a range first limited to North Carolina to Georgia, the distribution was later extended to Massachusetts by Gray (1886), and to Nova Scotia (disjunct) and Florida by Fernald (1936).

The nomenclatural history of *Solidago latissimifolia* is a circular path leading back to that name as the antecedent epithet for Elliott's Goldenrod. Before we present the synonymy, we feel that a sardonic quote from Fernald (1936, pp. 206–207) is in order:

> "It is a commonplace to note that long continued cultivation of plants, particularly if they be of naturally plastic groups and placed side-by-side with scores of their relations, renders them in some ways unlike the indigenous ancestors from which they were in the past derived. This observation, though trite, is important in connection with the species of *Solidago* early proposed in Europe from plants which had long grown in gardens. In his masterly and cautious life-long studies of the genus Asa Gray repeatedly commented on the impossibility of satisfactorily identifying with wild American plants most of the garden forms described by Willdenow, Miller and some other European authors. Occasionally the types of species described by Aiton from plants not too long grown and mixed with other species at Kew can be safely identified; but too many of Miller's types, from plants long grown in the old Chelsea Gardens, *are better allowed to sleep where they lie*" [emphasis added].

Should we have been intimidated by this admonition? A century ago, even a half-century, perhaps; nowadays, no. Times change; in his day, Gray did not have the benefit of the modern Code to aid him in simplifying the understanding of *Solidago* species, nor did he seem firmly bound by the principle of priority. Note his vacillating treatment of *Solidago elliptica* above. In one paper it is an American species; four years later, in another, it is an untraceable European cultivar. One hundred years after Gray finished his work, collections have increased massively and communication has become much more rapid. Tracing the origin of cultivars can be approached with less trepidation than formerly. It is no longer absolutely necessary, nor advisable, to let perplexing nomenclatural problems "sleep where they lie."

With few exceptions, European goldenrod cultivars have their ancestry in North American species. In pre-Linnaean days, European botanists and horticulturists were strongly attracted to the

profuse variety of North American goldenrods as potential garden plants and introduced many species into European gardens, to the continuing pleasure of European gardeners. Europeans still regard them highly, as opposed to the usual American disdain for these showy plants as "weeds" and "hayfever plants."

In time, treatments of Elliott's Goldenrod in regional floras such as Cronquist's (1980), have come to join Gray's concepts of *Solidago elliptica* and *S. elliottii* into a single species. Uttal has observed specimens representing both of Gray's concepts in a single population in Virginia. Vigorous shoots tend to have large open panicles; less vigorous shoots *from the same clone* tend to have tighter panicles. Some morphological trends have been associated with geography, as in the varieties proposed by Fernald (1936). These trends, however, are inconsistent, so much so that we only note them without taxonomic recognition. Environmentally induced variations in morphology, including apparent insect damage resulting in aborted inflorescences, are as common in Elliott's Goldenrod as they are in most other members of this plastic genus. This single concept is properly named *Solidago latissimifolia*, following the principle of priority.

TAXONOMY

Solidago latissimifolia Miller, Gard. Dict., ed. 8. 1768. LECTOTYPE (here designated): Jardin du Roi, Paris, *W. Houston* (photo, ex BM!).

Solidago elliptica Aiton, Hort. kew. 3:214. 1789. LECTOTYPE (here designated): *idem atque S. latissimifolia* (photo, ex BM!). PARALECTOTYPE: Kew, 1778 (photo, ex BM!).

Solidago elliptica ? Elliott, Sketch Bot. S. Carolina 2:376. 1824, *non* Aiton. HOLOTYPE: Parris Island, *S. Elliott* (NY, not seen); fragments, (GH!).

Solidago elliottii Torrey & Gray, Fl. N. Amer. 2:218. 1841. LECTOTYPE [designated by Fernald (1936)]: *idem atque holotypus supra*. PARALECTOTYPES: [Cape Fear] North Carolina, *M. A. Curtis* (NY!); Georgia, *Le Conte* (GH!).

Solidago elliptica Aiton var. *axilliflora* Gray, Proc. Amer. Acad. Arts. 27:181. 1882. HOLOTYPE: *idem atque holotypus S. latissimifolia*.

Solidago edisoniana Mackenzie in Small, Fl. S.E. U.S. ed. 3, 1358. 1933. HOLOTYPE (one specimen on three sheets): hammocks, near Fort Mead, Florida, *Moore 502*, 1 Jan. 1930 (NY!).

Solidago mirabilis Small, Fl. S.E. U.S. ed. 3., 1359. 1933. HOLOTYPE: Turnbull Hammock, N of Titusville, Brevard Co., Florida, *J. K. Small & C. A. Mosier*, 17 Dec. 1927 (NY!).

Solidago elliottii var. *ascendens* Fernald, Rhodora 38:215. 1936. HOLOTYPE: sandy thicket, Harwich, Massachusetts, *M. L., Katherine, & H. G. Fernald* (Pl. Exsicc. Gray. No. 492), 21 Sep. 1927 (GH!). ISOTYPES: (NY!, PH!, US!).

Solidago elliottii var. *pedicillata* Fernald, Rhodora 38:215. 1936. HOLOTYPE: border of wet pine woods, Eastville, Northampton Co., Virginia, *Fernald & Long 5526*, 12 Oct. 1936 (GH!). ISOTYPES: (NY!, US!).

Solidago elliottii var. *edisoniana* (Mackenzie) Fernald, Rhodora 38:216. 1936. BASIONYM: *Solidago edisoniana* Mackenzie.

Excluded species:

Solidago elliottii var. *divaricata* Fernald, Rhodora 17:7. 1915. HOLOTYPE: meadow northeast of Fresh Pond, Block Island, Rhode Island, *Fernald, Long, & Torrey 10,543*. 15 Sep. 1913 (GH!). ISOTYPE: (PH!). (3D) = *Solidago rugosa* var. *villosa* (Pursh) Fernald.

Solidago fragrans Willdenow [*Enum. suppl.* 59. 1809. LECTOTYPE (designated Jackson (1895): *Gerhard* (B, not seen)] is identified with *S. elliptica* Aiton by Jackson (1895) in Index Kewensis. The leaves are said to be triplinerved, which is not characteristic of *S. elliptica*. A Pursh specimen annotated with this name at PH! is *S. gigantea* Aiton.

According to Gray in Torrey and Gray (1841) and Gray (1886), several names may have been given to cultivated plants of *Solidago latissimifolia* in Europe in earlier times: *S. dubia* Scopoli [Fl. Insub. 2, 19, t. 10. 1786] ; *S. lateriflora* Willdenow [Sp. Pl. 3: 2057. 1803, *non* Linnaeus, *non* Aiton]; *S. verrucosa* Schrader [Hort. Goett t. 6. 1809]; and *S. cleliae* DeCandolle [Prod. 5:. 331. 1836]. We have not seen the types of any of these taxa, but none of these names is older than that of Miller.

COMMENTS

The material we borrowed from herbaria is mostly from the late 19th and early 20th centuries. Recent collections are remarkably scarce, particularly from metropolitan and resort areas. This scarcity clearly indicates that the habitat requirements of this valuable and showy goldenrod are in fierce competition with human interests. This observation was bolstered by field searches, which were largely unproductive, although they were not as exhaustive as we would have liked. It appears that *Solidago latissimifolia* has changed from a once common goldenrod of the North American outer Atlantic Coastal Plain to a dwindling species, threatened or

even endangered in some states. It is recommended that conservation action be taken in selected sites to alter an otherwise bleak future for this beautiful species.

In the course of this study, a number of misidentifications of *Solidago rugosa* var. *sphagnophila* Graves as *S. elliottii* were noted. The former taxon has smaller heads [3.0(5.5) mm high] on elongate spray-like racemes in leafless open panicles. Heads in *S. elliottii* are (3.5–)6.5 mm high. The heads also are usually more numerous in *S. rugosa* var. *sphagnophila*, and the involucral bracts are to 4 mm long and 0.6 mm wide, with tapering sides to an acute-attenuate tip. Those bracts of *S. latissimifolia* (*S. elliottii* Gray) are to 6 mm long and 1.2 mm wide, with parallel sides and obtuse tips. The leaves of the former are doubly serrate; those of the latter singly serrate. The glabrous var. *sphagnophila* is readily separable from *S. rugosa* Aiton var. *rugosa*; Uttal has found the former growing in North Carolina with *S. rugosa* var. *aspera* (Aiton) Fernald without introgression.

Present *Solidago* keys in regional manuals derive *S. rugosa* var. *sphagnophila* separately from the other varieties of the species; this system is awkward. We agree with Cronquist (Gleason & Cronquist, 1963, p. 175) that this taxon is "perhaps better called a distinct species, *Solidago aestivalis* Bicknell," as Seymour (1982) treated it. Present keys would only require substitution of the species name for the varietal one.

We also agree with Fernald (1950) that *Solidago aestivalis* occurs from southern Maine to North Carolina [Hoke County, Buffalo Creek slough at County Road 1214, *L. J. Uttal 13,461*, 24 Sep. 1984 (VPI!); Harnett County, roadside, State Road 87, 3.9 miles southeast of Sprout Spring, *H. Laing 536*, 4 Oct. 1956 (NCU!)]. In addition, a specimen has been found from South Carolina, which is an extension of range and a new state record [Horry County, edge of swale on junction of US 17 and N. 70th St., North Myrtle Beach, *J. A. Duke 0022*, 19 Oct. 1957 (NCU!)].

ACKNOWLEDGMENTS

The curators of BM, GH, NCU, NY, PH, US, and VPI are gratefully thanked for the generous loan of specimens, including types, and for access to facilities visited. We are particularly grateful to Mr. A. O. Chater of the British Museum (Natural History) for his essential contribution to this publication in supplying meticulous descriptive details and sketches from specimens, lifesize photocopies

of type specimens and literature, and for the excellent photographs of types (Figures 1, 3). Porter examined the material in the British Museum (Natural History); Uttal, however, is responsible for all determinations relative to this paper. Porter's visit to London was funded by a grant from the National Geographic Society.

LITERATURE CITED

Aiton, W. 1789. Hortus kewensis. 3 vols. George Nicol, London.

Cronquist, A. 1980. Vascular Flora of the Southeastern United States. Vol. 1. Asteraceae. University of North Carolina Press, Chapel Hill, NC..

Elliott, S. 1824. Sketch of the Botany of South Carolina and Georgia. 2 vols. J. R. Schenk, Charleston, SC.

Fernald, M. L. 1936. Contributions from the Gray Herbarium of Harvard University No. CXIII. VI. Studies in *Solidago*. Rhodora 38: 201-229.

_____. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York.

Gleason, H. A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand, New York.

Gray, A. 1882. Contributions to North American botany. I. Studies of *Aster* and *Solidago* in older herbaria. Proc. Amer. Acad. Arts 17:.163 230.

_____. 1886. Synoptical Flora of North America. Ivison, Blakeman, Taylor, and Co., New York.

Jackson, B. D. 1895. Index Kewensis. Vol. 1, fasc. 4. Clarendon Press, Oxford.

Linnaeus, C. 1753. Species plantarum. 2 vols. Impensis Laurentii Salvii, Stockholm.

Mackenzie, K. K. 1928. *Solidago flexicaulis* and *Solidao latifolia*. Rhodora 30: 223-224.

Miller, P. 1768. The Gardener's Dictionary. ed. 8. P. Miller. London.

Plukenet, L. 1694. Almagestum botanicum. L. Plukenet. London.

Porter, D. M. 1987. Paralectotypes and lectoparatypes. Taxon 36:435-436.

Seymour, F. C. 1982. The Flora of New England. 2nd ed. Phytologia Memoirs V. Plainfield, NJ.

Small, J. K. 1933. Flora of the Southeastern United States. 3rd ed. J. K. Small. New York.

Torrey, J. and A. Gray. 1841. A Flora of North America. Vol. 2, pt. 1. New York.

DEPARTMENT OF BIOLOGY
VIRGINIA POLYTECHNIC INSTITUTE & STATE UNIVERSITY
BLACKSBURG, VIRGINIA 24061

RHODORA, Vol. 90, No. 862, 1988

A MONOGRAPH OF *HYDROLEA* (HYDROPHYLLACEAE)

L. J. DAVENPORT

ABSTRACT

Hydrolea, a genus of purple- and white-flowered semi-aquatic herbs and shrubs, was last revised in 1913. After examination of available herbarium specimens, SEM of seed coat morphology, and fieldwork in Mexico, Venezuela and Ecuador, a monograph of *Hydrolea* is presented. In this treatment, two sections for the genus are maintained. Eleven species are recognized, with one species having three varieties.

Key Words: *Hydrolea,* Hydrophyllaceae, monographs, Eastern Hemisphere, Western Hemisphere

Hydrolea is a genus of semi-aquatic dicotyledonous plants. The genus is included in the family Hydrophyllaceae and is the only genus of aquatic or wetland plants of that family.

Hydrolea is native to eastern North America, Central America, the Caribbean Islands, South America, Central Africa and tropical Asia. Species are generally restricted in distribution to a single biogeographic region, although a few weedy species are naturalized in additional areas (Backer, 1951; Gibson, 1967; Jayasuriya, 1976). Due to its broad distribution, *Hydrolea* is a component of many floras and has been treated in many floristic works. Recent regional treatments of the genus have been included in Standley (1928), Small (1933), Williams (1947), Fernald (1950), Backer (1951), Lemée (1953), Gleason & Cronquist (1963), Croat (1967), Gibson (1967), Radford et al. (1968), Correll & Johnston (1970), Gibson (1970), Adams (1972), Correll & Correll (1972), Long & Lakela (1976), Nash (1979), Raynal-Roques (1980) and Godfrey & Wooten (1981).

Despite its availability to workers throughout the world and its occurrence in so many floras, *Hydrolea* has not been examined taxonomically for 70 years. This study was undertaken, then, in order to produce a thorough taxonomic revision of *Hydrolea.*

TAXONOMIC HISTORY

The taxonomic history of *Hydrolea* is confusing, due to its intertwining with that of *Nama.* Linnaeus (1753) first described *Nama,* based on *N. zeylanica,* placing it in the Pentandria Digynia

of his sexual system. Six years later a second species, *N. jamaicense*, was added (Linnaeus, 1759). Linnaeus (1762) then described the genus *Hydrolea*, based on *H. spinosa*, and placed this taxon in the Pentandria Digynia as well.

The two Linnaean species of *Nama* were early recognized as representing different genera; they were also seen to be closely related to *Hydrolea*. *Nama zeylanica* was transferred to *Hydrolea* by Vahl (1791), leaving *N. jamaicense* as the only species of *Nama*. While this treatment of the two genera has been generally accepted, Kuntze (1891) noting the transfer of the generic type of *Nama* to *Hydrolea*—replaced the name *Hydrolea* with that of *Nama* and proposed the name *Marilaunidium* to encompass those species formerly called *Nama* (including *N. jamaicense*). The International Botanical Congress at Vienna, however, voted to conserve the names *Hydrolea*, based on *H. spinosa* and including *N. zeylanica*, and *Nama* based on *N. jamaicense* (Wettstein et al., 1906). Despite this ruling, the followers of the American Code continued to use the name *Nama* for the genus *Hydrolea*. This usage is reflected in Britton and Brown (1896, 1913) and in Small (1903, 1913, 1933), and is apparent on many herbarium sheets.

As indicated by their interwoven taxonomic histories, *Hydrolea* and *Nama* are morphologically similar, and so have often been treated as "sister" genera. Based largely on their sympetalous corollas, De Jussieu (1789) assigned *Hydrolea* and *Nama* to what is now the Convolvulaceae. Brown (1818) placed these two genera in a distinct group, Hydroleae (later Hydroleaceae), to which Dumortier (1829) added *Wigandia*. The segregation of these genera as a separate family was maintained by Choisy (1833, 1846) in the first major works on these plants. Gray (1875) later merged Hydroleaceae with Hydrophyllaceae, placing *Nama* in the tribe Nameae and *Hydrolea* in the Hydroleae; such placement is presently accepted (e.g., Bentham & Hooker [1876], Brand [1913]).

Besides *Nama*, a number of generic names have been applied to *Hydrolea*. Soon after describing both *Nama* and *Hydrolea*, Linnaeus (1767) contributed the genus *Steris*, apparently basing it on a specimen of *N. zeylanica* from Java. The appearance of occasional trilocular forms often proved confusing to early workers and led to the descriptions of *Sagonea* by Aublet (1775) and *Reichelia* by Schreber (1789). While recognizing its close affinities to *Hydrolea*, Thouars (1806) described the homonym *Hydrolia* as a separate genus due to supposed differences in the insertion of the stamens. Rafinesque (1838) added the genus *Ascleia*, listing *Lycium capsulare*

[*Hydrolea spinosa* var. *spinosa*] as a synonym of the type species. Finally, Hasskarl (1842) contributed *Beloanthera*, based on a plant with opposite leaves, which both Backer (1931) and Van Steenis (1948) have considered to be synonymous with *Hydrolea*.

Hydrolea was first extensively studied by the Swiss botanist Choisy. In his initial study, Choisy (1833) described two new species and listed a total of eight species in the genus. In a later work, Choisy (1846) included 11 species in *Hydrolea*, two of these being new. Bennett (1871a) described three new species, bringing the total number that he recognized to 12. Brand (1913) described two new species and separated the genus into two sections based on geography and placental characteristics: section *Attaleria*, containing five Eastern Hemisphere species with unlobed placentas, and section *Sagonea*, containing 14 Western Hemisphere species with lobed placentas. Brand also recognized numerous infraspecific taxa, including nine varieties, one subvariety and six forms. Additional taxa have since been described by Hassler (1914), Brand (1927) and Nash (1979). New combinations and nomenclatural changes have been proposed by Macbride (1917) and Fernald (1944).

MORPHOLOGY AND LIFE HISTORY

HABIT. Species of *Hydrolea* are herbs or small shrubs, usually growing near water, with roots and lower stems often submerged. Mature plants are perennial, or occasionally annual; overwintering is by stem bases or as seeds. Spring growth arises from the uppermost viable buds. Prostrate stems may act as rhizomes or runners, with growth from the lower nodes developing into new culms; adventitious roots may arise from submerged nodes as well.

While most individuals of *Hydrolea* exhibit an ascending or erect habit, prostrate and dwarf growth forms may occur. These forms have at times been treated as distinct taxa, especially in the case of variants of *H. zeylanica*. Exell (1929), for example, treated a prostrate form of *H. zeylanica* from Angola as a new species, *H. prostrata*. Based on habit, Haines (1922) described vars. *erecta* and *diffusa* of *H. zeylanica*; these varieties were maintained by Banerji et al. (1974). Merrill (1918) recognized the ecological basis for this variability, stating that the prostrate or dwarfed form of *H. zeylanica* is characteristic of drying-out pools and rice paddies. In a similar case, *Hydrolea multiflora*, which is profusely branched and spreading in habit, appears to represent a dwarfed form of the more erect *H. elatior*.

STEMS. Stems are succulent to woody, usually green or brown but sometimes dark purple to nearly black. Purple-stemmed forms of *Hydrolea spinosa* were designated by Brand (1913) as var. *spinosa* f. *purpurascens*; the nearly black stems of *H. nigricaulis* account for the specific epithet of that species. Stems may be glabrous, puberulent or densely pubescent, with or without glandular trichomes or long, jointed hairs. While examining trichomes in the Polemoniales, Inamdar & Patel (1973) described four types of capitate, filiform, glandular trichomes in *H. zeylanica*: those with uniseriate heads, globular multicellular heads, fusiform multicellular heads, and clavate multicellular heads.

LEAVES. Leaves are generally lanceolate or ovate, although nearly linear in one variety of *Hydrolea spinosa* and distinctly linear in *H. floribunda*. Margins are entire or serrulate, and often undulate (as in *H. spinosa* var. *maior, H. quadrivalvis* and *H. uniflora*). Surface pubescence usually parallels the pubescence of the stems, being glabrous, puberulent or densely pubescent, with or without glandular trichomes or long, jointed hairs. Pubescence of the abaxial surface is generally less than that of the adaxial surface; in some cases hairs are restricted to the main veins of either surface. Apices are usually acuminate or acute, but are rounded in some specimens of *H. zeylanica*. Bases are attenuate or acute, although obtuse to cordate-clasping in *H. macrosepala*; petioles may be present or absent.

THORNS. Thorns, if present, are borne nodally, usually one or two per node. In rare cases the thorns may be branched with a shorter, secondary thorn arising from the base of the primary one. Although historically these sharp-pointed structures have been referred to as "spines," the frequent presence of small leaves at their tips reveals them to be modified branches rather than leaves.

The presence (or absence) and abundance of thorns have long been treated as important characters in *Hydrolea* taxonomy, as indicated by the specific epithet of the type species, *H. spinosa*. Choisy (1833, 1846) divided the genus into two groups based on presence or absence of thorns, and this method was later followed by Bennett (1871a). Brand (1913) did not split the genus on the basis of thorns, but he recognized many subspecific taxa, especially of *H. spinosa*, on the basis of thorn characteristics.

As suggested by Macbride (1917), thorn production may be a Mendelian trait. This explanation would readily account for the

occasional appearance of thornless forms of usually thorny species, as in *H. quadrivalvis* and *H. uniflora*. Certain taxa, however, have entirely lost the ability to produce thorns. This split between thorny and thornless species must have occurred early in the evolution of the genus, because thorny species occur only in the Western Hemisphere and most thornless ones in the Eastern Hemisphere.

INFLORESCENCES. Both terminal and axillary inflorescences are found in *Hydrolea*. The terminal inflorescences have been described as corymbs, cymes, cincinni and panicles. True corymbs are found in *H. floribunda, H. corymbosa* and *H. ovata*, with panicles more characteristic of *H. zeylanica, H. elatior* and *H. macrosepala*. Inflorescences of *H. spinosa* appear almost axillary in some Central American populations (tending toward var. *maior*), while in other populations, especially in southeastern South America, corymbs or panicles are more prominent (tending toward var. *paraguayensis*). In *H. spinosa* var. *maior* the flowers are often borne in tight clusters at the branch tips; in some populations (formerly segregated as *H. mollis*) of *H. spinosa* var. *paraguayensis* a unique, dense panicle is found.

Axillary inflorescences in *Hydrolea* have been described as cymes, fascicles, and glomerules. Among the species producing axillary inflorescences, *H. palustris* and *H. nigricaulis* have only a few flowers at each node, while *H. quadrivalvis* and *H. uniflora* have up to 10 flowers per node. While the axillary inflorescences of *H. palustris*, *H. quadrivalvis* and *H. nigricaulis* are nearly sessile, the inflorescences of *H. uniflora* are usually borne on long (up to 4 cm) peduncles. These long peduncles are especially common at the lower nodes of fruiting plants.

In some specimens of species with axillary inflorescences, flowering side branches may develop as well, resulting in a panicle-like inflorescence. The occasional occurrence of these highly branched forms suggests that axillary inflorescences in *Hydrolea* evolved by suppression and compaction of widely branched panicles.

FLOWERS. Flowers of *Hydrolea* are perfect. The sepals are lanceolate in all species except *H. macrosepala*, in which they are distinctly cordate. Sepal surfaces may be glabrous, puberulent, densely pubescent or hispid-hirsute, with or without glandular trichomes or long, jointed hairs. Sepal margins are entire.

The bases of the petals are connate, forming a five-lobed campanulate corolla. Corollas are bright blue or purple in all species

except *Hydrolea nigricaulis*, in which they are white; white flowers are occasionally found in populations of blue-flowered species. In blue and purple flowers the base of the corolla tube is often white; a white stripe may also be apparent along the midveins of the petals.

Five stamens, with dilated filament bases, are inserted at the base of the corolla tube. Anthers are pale pink, white or blue, with white or blue filaments.

The rounded ovaries are usually bilocular. The aberrant condition of trilocular ovaries has been frequently observed, leading to the designation of such taxa as *Hydrolea trigyna* Swartz (1788). I have also observed four-loculed forms, a condition that is most apparent in specimens of *H. spinosa*.

Two white, brown or blue styles with slightly funnelform stigmas arise from the top of each ovary. As might be expected, ovaries with three or four locules also have three or four styles. *Sagonea* [*Hydrolea*] *palustris* is illustrated as having three styles (Aublet, 1775).

Hydrolea ovules are borne on axile placentas, which may be lobed or entire. As mentioned previously, Brand (1913) used placental characters, along with distributional data, to divide the genus into sections *Sagonea* [*Hydrolea*] and *Attaleria*.

Mitra (1945, 1947) studied the development of the female gametophyte and embryo of *Hydrolea zeylanica*. According to these studies, the placentas have numerous anatropous ovules attached, and a poorly developed nucellus is formed. A normal eight-nucleated embryo sac develops from a single functional megaspore mother cell. The nucellus disintegrates during development of the embryo sac, and a jacket layer is formed. Fertilization is porogamous.

The pollen of *Hydrolea* has been examined only recently. Constance & Chuang (1982) examined *Hydrolea* pollen as part of their survey of hydrophyllaceous pollen morphology, finding that *Hydrolea* pollen grains are tricolporate, with smooth colpi and reticulate exines. Pollen may be white or yellow.

Fruits. The fruits of *Hydrolea* are usually bilocular, multiseeded capsules; three- and four-loculed forms are also encountered. The styles are persistent in fruit, although Bennett (1871a) stated that deciduous styles are the general case in *H. elegans*. The capsules, as well as the attached styles, are light brown to dark blue when mature and may be glabrous, puberulent or glandular-pubescent.

SEEDS. *Hydrolea* seeds are ovoid to cylindrical in shape, light to dark brown when mature, and marked by longitudinal ridges. Seeds of *H. zeylanica* and *H. corymbosa* have distinct lateral ridges as well. Kainradl (1927) found that the testa of *H. spinosa* seeds is composed of an epidermal layer, a brownish lamella, and epithelial cells. Seeds, as viewed under SEM, are marked by prominent reticulation patterns, with either uniformly broad reticulations, narrowed reticulations lacking ornamentation, or narrowed reticulations with papules or "doughnuts" at the reticulation joints. Representative seeds are shown in Figures 1 and 2.

Bennett (1871a) depicted his new species, *Hydrolea elegans*, as having seeds with membranous wings. This character would certainly be unique in *Hydrolea*, but I have found no specimens illustrating the trait. The condition depicted by Bennett may, instead, be an aberrant one arising from the adherence of placental material to the seed coat.

In one of the few studies of the biology of the genus, Kainradl (1927) discovered that the seeds of *Hydrolea spinosa*, although heavier than water, remain afloat for several days and are thus subject to distribution by currents or waterfowl. Light is necessary for their germination, with darkness and blue light hindering germination. Kainradl also determined that *H. spinosa* seeds may germinate while floating as well as while covered by substrate.

CHROMOSOME NUMBERS. Chromosome numbers have been established for a few species of *Hydrolea*, especially those occurring in the Western Hemisphere. Cave & Constance (1959) determined $2n = 20$ for *H. quadrivalvis*. This number was verified by Constance (1963), who added similar counts of $2n = 20$ for *H. affinis* [*H. uniflora*] and *H. ovata*. Svensson (1925) reported a count of $2n = 40$ for *H. spinosa*; I have also obtained this count for a Venezuelan population (*Davenport 1686*) of this species. Lincoln Constance (pers. comm.) has an unpublished count of $2n = 20$ for an unarmed specimen of *H. spinosa*.

While the Western Hemisphere taxa appear to have a base number of 10, the Eastern Hemisphere taxa may have a base number of 9 or 12. *Hydrolea zeylanica*, however, is the only Eastern Hemisphere species to have been examined in this regard. A count of $n = 9$ [$2n = 18$] was published by Datta & Manna (1963) as well as by Sarkar et al. (1973); a count of $2n = 24$ has also been published for the same species (Krishnappa, 1971).

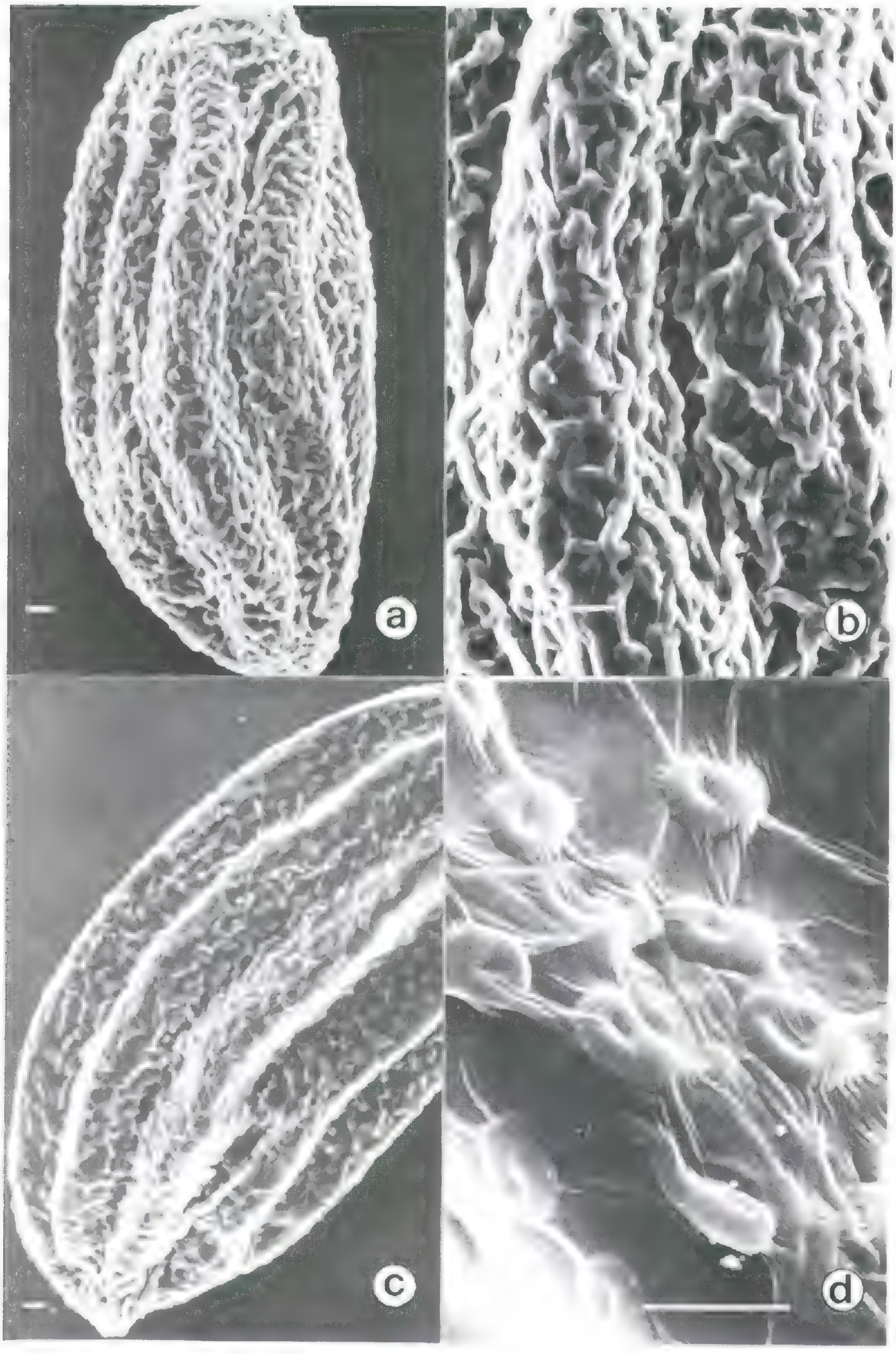


Figure 1. Surface morphology of *Hydrolea floribunda* (a, b) and *H. palustris* (c, d) seeds. Lines equal 10 μm.

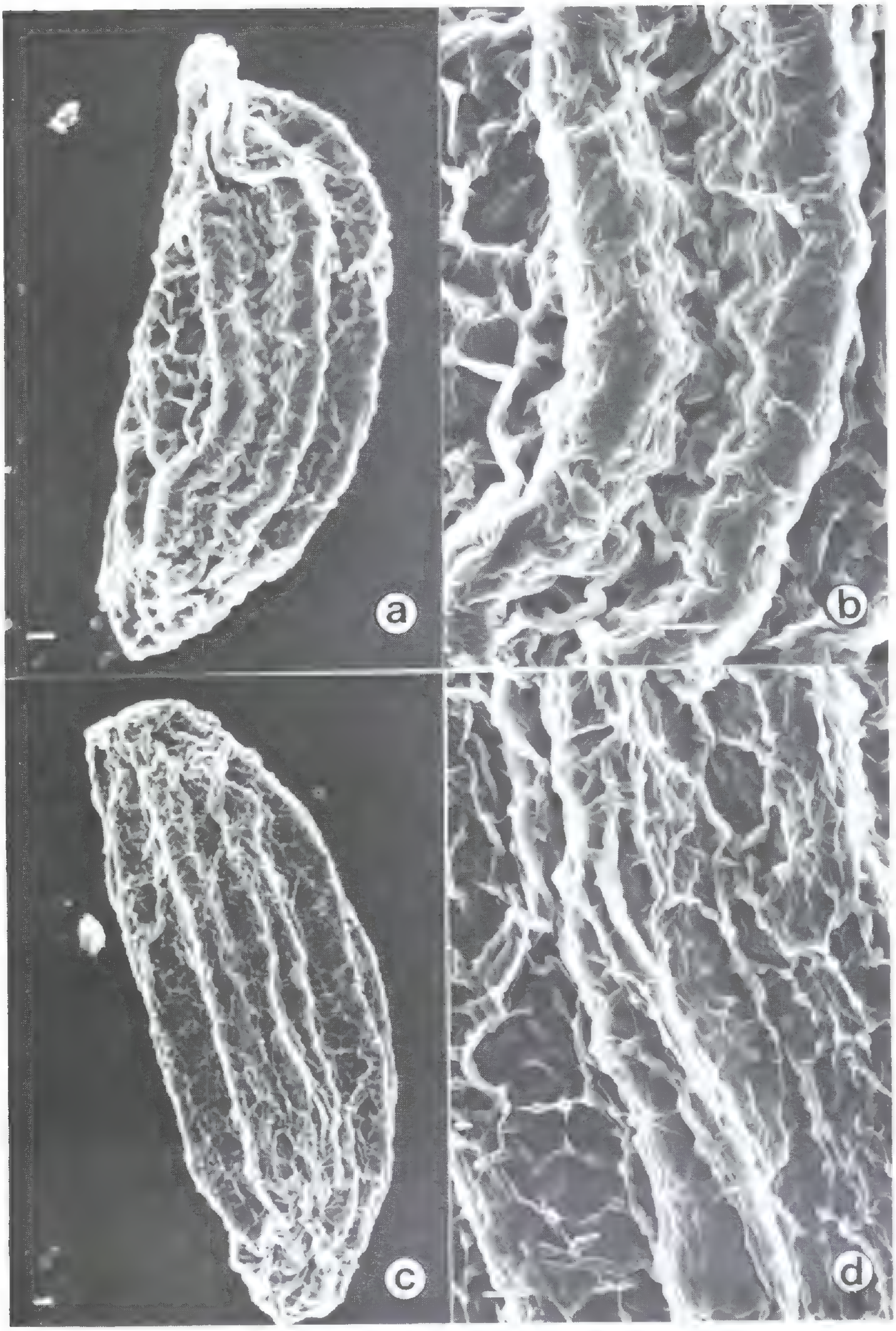


Figure 2. Surface morphology of *Hydrolea nigricaulis* (a, b) and *H. ovata* (c, d) seeds. Lines equal 10 μm.

TAXONOMIC TREATMENT

Hydrolea L., Sp. pl. ed. 2, 328. 1762 (nom. cons.). TYPE: *H. spinosa* L.

Nama L., Sp. pl. 226. 1753 (non *Nama* L., Syst. nat. ed. 10, 950. 1759). TYPE: *N. zeylanica* L. ("Zaylanica").

Steris L., Syst. nat. ed. 12, 2:140, 196. 1767; Mant. pl. 8, 54. 1767 (non *Steris* Adanson, Fam. pl. 2:255, 607. 1763). TYPE: *S. javana* L.

Sagonea Aublet, Hist. pl. Guiane 1:285. 1775. TYPE: *S. palustris* Aublet.

Reichelia Schreber, Gen. pl. ed. 8, 200. 1789 (nom. superfl., because *Sagonea* ("Sagona") was cited in synonymy).

Reichela Cothenius, Disp. veg. meth. 11. 1790 (orth. var.).

Hydrolia Thouars, Gen. nov. madagasc. 9. 1806. TYPE: *H. madagascariensis* Choisy (Mém. Soc. Phys. Genève 6: 111. 1833).

Hydrolaea Dumortier, Anal. fam. pl. 25. 1829 (orth. var.).

Ascleia Raf., Sylva tell. 53. 1838. TYPE: *A. mexicana* Raf. (nom. superfl., because *Lycium capsulare* was listed in synonymy).

Beloanthera Hasskarl, Flora 25:55. 1842. TYPE: *B. oppositifolia* Hasskarl.

Perennial, occasionally annual, semi-aquatic herbs or small shrubs, to 2 m tall; erect, prostrate or decumbent, unbranched or highly branched, often gregarious, with new culms arising from prostrate stems. Stems succulent to woody, the bases often swollen by spongy aerenchyma tissue, green, brown, purple or black, glabrous to hispid-hirsute, with or without glandular trichomes or long, jointed hairs. Leaves alternate, exstipulate, pinnately veined, ovate, lanceolate or linear, 1–12 cm long, 2–30 mm wide, glabrous to densely pubescent, sometimes gland-dotted, with or without glandular trichomes or long, jointed hairs, occasionally pubescent only along the main veins; margins entire or serrulate, often undulate; apices acuminate, acute or rounded; bases attenuate, acute, rounded or cordate-clasping, sessile or tapering to a short (to 1 cm long) petiole. Thorns 1–2 per node or absent, 4–30 mm long, 0.2–2 mm broad, occasionally bearing small leaves toward tips. Flowers on short (to 1 cm long) pedicels, borne in terminal corymbs, clusters at branch tips, leafy panicles, axillary fascicles (from compacted branchlets) on peduncles up to 4 cm long, or singly in leaf axils. Sepals 5, equal, separate, persistent in fruit, lanceolate, ovate or cordate, 2.5–12 mm long, 0.4–7.5 mm wide, glabrous to hispid-hirsute, with or without glandular trichomes or long, jointed hairs, the margins entire. Corolla campanulate, white, purple or blue (purple and blue flowers occasionally lighter at bases and along petal midveins); petals 5, equal, imbricate in bud, connate at the bases, 2.5–17 mm long, 0.6–12 mm wide. Stamens 5, equal, free, exserted or included,

alternate with petals, inserted on the short corolla tube, the filaments filiform, abruptly dilated at bases, white or blue, glabrous; anthers 4–lobed, dorsifixed, pale pink, white or blue, dehiscing longitudinally; pollen tricolporate, with smooth colpi and reticulate exine, white or yellow. Disc absent. Ovary superior, globose to subglobose, green or blue, the lower half glabrous, the upper half glabrous, puberulent or glandular-pubescent; placentation axile, the placentas adnate to a thin septum, spongy, entire or bifid in cross-section, bearing numerous anatropous ovules; styles 2–4, equal, separate, often inarched at summits, white, brown or blue, persistent in fruit, 0.5–15 mm long, glabrous, puberulent or glandular-pubescent (especially at bases); stigmas funnelform. Capsule globose, subglobose or cylindrical, occasionally truncated at style bases, brown or purple, erect or drooping at maturity, dehiscing septicidally, loculicidally or irregularly, 2 8 mm long, 1.5–7 mm broad, the lower half glabrous, the upper half glabrous, puberulent or glandular-pubescent. Seeds numerous, ovoid to cylindrical, symmetrical or occasionally asymmetrical, tan to dark brown, 0.3–0.7 mm long, 0.1 -0.4 mm broad, with longitudinal and (more rarely) transverse ridges; reticulations prominent, uniformly broad or narrowing at the joints, the joints with or without papules, circles or half-circles. Chromosome number: n =9, 10 or 12. TYPE SPECIES: *H. spinosa* L. (From the Greek *hudor,* water, referring to the aquatic habitat).

Key to Sections of *Hydrolea*

1. Placenta of each locule lobed, divided into 2 wings; thorns present or absent; species native to Western Hemisphere ..... section *Hydrolea*
1. Placenta of each locule entire, not divided into 2 wings; thorns lacking; species native to Eastern Hemisphere ..... section *Attaleria*

In the first major work involving *Hydrolea*, Choisy (1833) divided the genus on the basis of presence or absence of thorns. This method of treatment was continued in a later work by Choisy (1846) and was also adopted -although with reservations—by Bennett (1871a). Brand (1913) established formal sections for the genus, doing so on the basis of placental and geographical differences; his treatment, however, closely parallels the previous ones, which were based on thorns.

Although *Hydrolea* may seem too small a genus to warrant infrageneric divisions, I have retained Brand's classification for three reasons. First, the two sections form natural morphological sets based on a constellation of minor character differences; placental type, presence or absence of thorns, flower size, and general pubescence are four such characters. Second, the geographical separation of the species is nearly total, with members of the two sections separated by a major obstacle to dispersal—the Atlantic Ocean. A third line of evidence, albeit based on limited samples, is the difference in base chromosome number between the two sections, with section *Attaleria* based on $n = 9$ or 12 and section *Hydrolea* based on $n = 10$.

Hydrolea section **Hydrolea**

Hydrolea section *Sagonea* (Aublet) Brand, Pflanzenr. 4, 251:177. 1913.

Herbs or small shrubs, to 2 m tall. Stems green, brown, purple or black, glabrous to hispid-hirsute, often bearing glandular trichomes or long, jointed hairs. Leaves ovate to lanceolate, occasionally linear, 1–12 cm long, 3–30 mm wide, glabrous to hispid-hirsute, with or without glandular trichomes or long, jointed hairs; margins entire or serrulate, often undulate; apices acuminate to acute, occasionally rounded; bases attenuate to acute, occasionally rounded. Thorns present or absent. Flowers borne in terminal corymbs, terminal clusters, leafy panicles, or short to long (up to 4 cm) pedunculate axillary fascicles. Sepals lanceolate to ovate, 2.5–14 mm long, 0.4–4 mm wide, glabrous to hispid-hirsute, with or without glandular trichomes or long, jointed hairs. Corolla blue or white, the petals 2.5 17 mm long, 0.5–12 mm wide. Ovary glabrous to puberulent, the upper half often glandular-pubescent; placentas bifid in cross-section; styles 2–4, 0.5–15 mm long, glabrous, puberulent, or glandular-pubescent. Capsule globose to cylindrical, erect at maturity, 2–8 mm long, 1.5–7 mm broad, the upper half glabrous, puberulent, or glandular-pubescent. Seeds ovoid to cylindrical, occasionally asymmetrical, 0.3–0.7 mm long, 0.1–0.4 mm broad, with longitudinal and (in one species) transverse ridges; reticulations uniformly broad or narrowing at the joints, the joints with or without papules, without circles or half-circles. Chromosome number: $n = 10$. LECTOTYPE SPECIES: *H. spinosa* L. (Lectotype here designated.)

KEY TO TAXA OF *HYDROLEA* SECTION *HYDROLEA*

1. Flowers borne in axillary fascicles 2
   2. Corolla white, the petals 2.5–4 mm long . . . . . 3. *H. nigricaulis*
   2. Corolla usually blue, the petals 7–11 mm long 3
      3. Stems and sepals with long, jointed trichomes . . . . . 7. *H. quadrivalvis*
      3. Stems and sepals glabrous to puberulent, lacking long, jointed trichomes . . . . . **6.** *H. uniflora*
1. Flowers borne in terminal corymbs or leafy panicles 4
   4. Styles 5 mm long or less; petals 8 mm long or less 5
      5. Thorns absent; capsules globose, 3–5 mm long . . . . . **2.** *H. elatior*
      5. Thorns present; capsules ovoid, 5–6 mm long . . . . . **1c.** *H. spinosa* var. *maior*
   4. Styles greater than 5 mm long; petals greater than 8 mm long 6
      6. Stems pubescent, with only occasional glandular trichomes 7
         7. Leaves densely pubescent; styles 10–15 mm long . . . . . **5.** *H. ovata*
         7. Leaves glabrous to puberulent; styles 5–10 mm long . . . . . **4.** *H. corymbosa*
      6. Stems glabrous to pubescent, usually densely covered by glandular trichomes 8
         8. Petals 13–17 mm long; sepals 7–14 mm long . . . . . **1b.** *H. spinosa* var. *paraguayensis*
         8. Petals 8–13 mm long; sepals 6–9 mm long . . . . . **1a.** *H. spinosa* var. *spinosa*

1. **Hydrolea spinosa** L., Sp. pl. ed. 2, 328. 1762.

Herbs or small shrubs, to 2 m tall, erect or decumbent, unbranched to broadly branched. Stems green, brown or purple, pubescent to hispid-hirsute, occasionally glabrous, usually densely covered with short, glandular trichomes. Leaves ovate to lanceolate, occasionally linear, 1–12 cm long, 2–30 mm wide, puberulent to hispid-hirsute, with or without glandular trichomes; margins entire or serrulate, often undulate; apices acuminate to acute; bases attenuate to acute. Thorns 1–2 per node or absent, 4–30 mm long, 0.4–2 mm broad. Flowers borne in narrow or broadly branching leafy

panicles or clustered at branch tips. Sepals lanceolate, 6–14 mm long, 1.5–3.5 mm wide, puberulent to hispid-hirsute, with glandular trichomes. Corolla blue, rarely white, the petals 5 17 mm long, 2–12 mm wide. Ovary puberulent, the upper half usually glandular-pubescent; styles 2–4, 1.5–13 mm long, glandular-pubescent toward bases. Capsule globose to ovoid, 3.5–8 mm long, 3–7 mm broad, the upper half puberulent or glandular-pubescent. Seeds ovoid to cylindrical, symmetrical, 0.4–0.7 mm long, 0.2 0.3 mm broad, with longitudinal ridges; reticulations narrowing at the joints, the joints with or without papules. Chromosome number: $n = 10$ (Constance, unpubl.), 20 (Davenport, unpubl.; Svensson, 1925).

Discussion. *Hydrolea spinosa* has long been noted as an extremely variable species. Specimens vary most noticeably in pubescence, thorniness, and leaf shape and size. Some workers have interpreted this variation as indicative of the presence of additional species; others have erected infraspecific taxa. Swartz (1788), for example, described *H. trigyna* due to its trilocular rather than bilocular capsules. Bennett (1871a) described *H. paludosa* on the basis of leaf shape and the recurving nature of the thorns; he also described *H. elegans* largely on the basis of its glabrous sepals and stems. Brand (1913) erected a complex series of infraspecific categories for *H. spinosa*, designating three varieties, one subvariety, and six forms.

Although much of the variation in *Hydrolea spinosa* seems to result from local environmental conditions, some trends in morphology can be discerned. Specimens from Central America are generally the most thorny and viscid, with more compact, raceme-like inflorescences and smaller flower parts. At the other extreme—both morphologically and geographically—specimens from southeastern South America have fewer or no thorns, more broadly branching inflorescences, larger flower parts, and are less viscid. *Hydrolea cervantesii*, described by Brand (1913) from Mexico, represents the northwestern end of a continuum of variation, while *H. megapotamica*, described by Sprengel (1827) from the Río de la Plata region, represents the southeastern end. Because of the continuous nature of this variation and the isolation of these two taxa at the geographical extremes of *H. spinosa*'s distribution, I have chosen to treat *H. cervantesii* and *H. megapotamica* as varieties of *H. spinosa* (vars. *maior* and *paraguayensis*, respectively).

1a. **Hydrolea spinosa** L. var. **spinosa**. TYPE: LINN? (not listed by Savage [1945]).

Lycium capsulare L., Cent. pl. II, 11. 1756. LECTOTYPE (here designated): Nova Hispania, without collection data or date, *Miller 5* (LINN; IDC 144: 259.8).

Hydrolea trigyna Swartz, Prodr. veg. Ind. occ. 54. 1788. LECTOTYPE (here designated): Without collection data, 1731, *Houston s. n.* (BM!; photographs of lectotype: UNA!). A note attached to this specimen perfectly matches Swartz's original description; the sheet is also labelled "Hydrolea trigyna."

Hydrolea glabra Choisy, Mém. Soc. Phys. Genève 6:110. 1833; non Schumacher, 1827. LECTOTYPE (here designated): Nova Hispania, without collection data or date, *Miller s. n.* (BM!; photographs of lectotype: UNA!).

Ascleia mexicana Raf., Sylva tell. 53.1838 (nom. superfl., because *Lycium capsulare* was listed in synonymy).

Hydrolea spinosa var. *elliptica* Miquel, Linnaea 18:597. 1845. TYPE: Not seen; possibly at U or L (Stafleu & Cowan, 1981).

Hydrolea extra-axillaris Morren, Ann. Soc. Roy. Agric. Gand 2:40. 1846. TYPE: Not seen; probably at LG (Stafleu & Cowan, 1981).

Hydrolea spinosa var. *inermis* Spruce ex A. W. Bennett, J. Linn. Soc., Bot. 11:269. 1871. LECTOTYPE (here designated): [BRASIL,] Tarapoto, Nov [18]55, *Spruce 4264* (K; photographs of lectotype: UNA!).

Hydrolea paludosa A. W. Bennett, J. Linn. Soc., Bot. 11:270. 1871. SYNTYPES: BRASIL, Tda do Pinhal, without date, *Sellow 703* (B [presumably destroyed]); BRASIL, ad Joao d'El Rey, without date, *Pohl 351* (W?); BRASIL, in uliginosis prope villam S. Salvador, without date, *Pohl 5358* (W?).

Hydrolea elegans A. W. Bennett, J. Linn. Soc., Bot. 11:271. 1871. HOLOTYPE: [BRASIL,] M[inas] G[erais], without date, *Martius 1698* (M; photographs of holotype: F!, GH!, UNA!).

Hydrolea spinosa var. *glabra* Martius ex A. W. Bennett, J. Linn. Soc., Bot. 11:272. 1871 (pro syn. sub *H. elegans*).

Hydrolea tetraginia Sessé & Mociño, Naturaleza (Mexico City) (ser. 2) 1, App. 44. 1888. TYPE: Not seen; possibly at MA (Stafleu, 1967). Specimens at BM and F are labelled as this species, and these specimens may represent duplicates of the type material.

Nama extra-axillaris (Morren) Kuntze, Revis. gen. pl. 2:435. 1891.

Nama paludosa (A. W. Bennett) Kuntze, Revis. gen. pl. 2:435. 1891.

Nama elegans (A. W. Bennett) Kuntze, Revis. gen. pl. 2:435. 1891.

Nama spinosa (L.) Kuntze, Revis. gen. pl. 2:435. 1891.

Hydrolea spinosa f. *trigyna* (Swartz) Voss, Vilmorin's Blumengartnerei ed. 3, 1:691. 1894.

Hydrolea tetragyna Pavon ex Brand, Pflanzenr. 4, 251:180. 1913 (pro syn. sub *H. spinosa*).

Hydrolea spinosa var. *spinosa* f. *purpurascens* Brand, Pflanzenr. 4, 251:182. 1913. SYNTYPES: [COLOMBIA,] Tolima, Feb 1883, *Lehmann 2579a* (B [now destroyed]; ISOSYNTYPE: BM!; photographs of isosyntype: UNA!); COLOMBIA, Bogotá, *Lehmann 4022* (B [now destroyed]; no isosyntypes located).

Hydrolea spinosa var. *spinosa* f. *glabra* (Choisy) Brand, Pflanzenr. 4, 251:182. 1913.

Hydrolea spinosa var. *paludosa* (A. W. Bennett) Brand, Pflanzenr. 4, 251:182. 1913.

Hydrolea spinosa var. *megapotamica* (Sprengel) Brand, Pflanzenr. 4, 251:182. 1913 (nom. superfl., because *H. spinosa* var. *inermis* was listed in synonymy).

Hydrolea capsularis (L.) Druce, Bot. Exch. Club Soc. Brit. Isles 3:419. 1914.

Hydrolea ovata var. *parvifolia* D. Nash, Fl. Veracruz fasc. 5:4. 1979. HOLOTYPE: MEXICO, Vera Cruz, 2 km adelante Panga, Río Tesechoacan, rumbo a Isla, 13 Apr 1969, *Nevling & Gómez-Pompa 830* (GH!; ISOTYPE: MEXU; photographs of holotype: UNA!).

Hydrolea ovata auct. non Nuttall ex Choisy: Bennett, Fl. bras. 7:396. 1871.

Herbs or small shrubs, to 2 m tall, erect or decumbent, usually broadly branched. Stems green, brown or purple, glabrous to hispid-hirsute. Leaves ovate to lanceolate, 1 12 cm long, 5 30 mm wide, pubescent, with or without glandular trichomes; margins entire or serrulate. Thorns 1–2 per node, rarely absent, often branched, 5–30 mm long, 0.5 2 mm broad. Flowers borne in narrow or broadly branching leafy panicles. Sepals lanceolate, 6 9 mm long, 1.5 3 mm wide, densely pubescent to hispid-hirsute. Petals 8 13 mm long, 5–7 mm wide. Styles 2–4, 4.5–7.5 mm long. Capsule globose to ovoid, 3.5 7.5 mm long, 3 5.5 mm broad. Seeds cylindrical, 0.6 0.7 mm long; reticulations narrowing at the joints, the joints with papules.

DISTRIBUTION. Widely distributed in the Western Hemisphere, from southernmost Texas to Argentina, and occasionally adventive in the Eastern Hemisphere. Flowering year-round. Figures 3 6, 9.

REPRESENTATIVE SPECIMENS. For this and the following taxa, a list of representative specimens will be sent upon request.

1b. **Hydrolea spinosa** var. **paraguayensis** (Chodat) Davenport, *comb. nov. Hydrolea paraguayensis* Chodat, Bull. Herb. Boissier 7, App. 1:78. 1899. HOLOTYPE: PARAGUAY, Guaropi dans les prairies marecageuses, 14 Mar 1881, *Balansa 3135* (G?; ISOTYPES: B [now destroyed], BM!, MO!, UC!; photographs of isotypes: F!, GH!, NY!, UC!, UNA!). *Hydrolea megapotamica* var. *paraguayensis* (Chodat) Macbride, Contr. Gray Herb. 49:46. 1917.

Hydrolea megapotamica Sprengel, Syst. veg. ed. 17, 4:114. 1827. TYPE: Not located and possibly destroyed, if at B (see Stafleu, 1967).

Nama megapotamica (Sprengel) Kuntze, Revis. gen. pl. 2:435. 1891.

Hydrolea mollis Chodat, Bull. Herb. Boissier 7, App. 1:78. 1899. SYNTYPES: PARAGUAY, [La Cordillera,] in dumetis San Bernardino, Dec 1885 1896, *Hassler 1572* (G); PARAGUAY, [La Cordillera?,] in dumetis pr. Jaguaron, Dec 1885 1896, *Hassler 1572a* (G).

Hydrolea paraguayensis f. *grandifolia* Chodat & Hassler, Bull. Herb. Boissier (ser. 2) 4:64. 1903. SYNTYPES: PARAGUAY, in stagnis pr. Valenzuela in valle

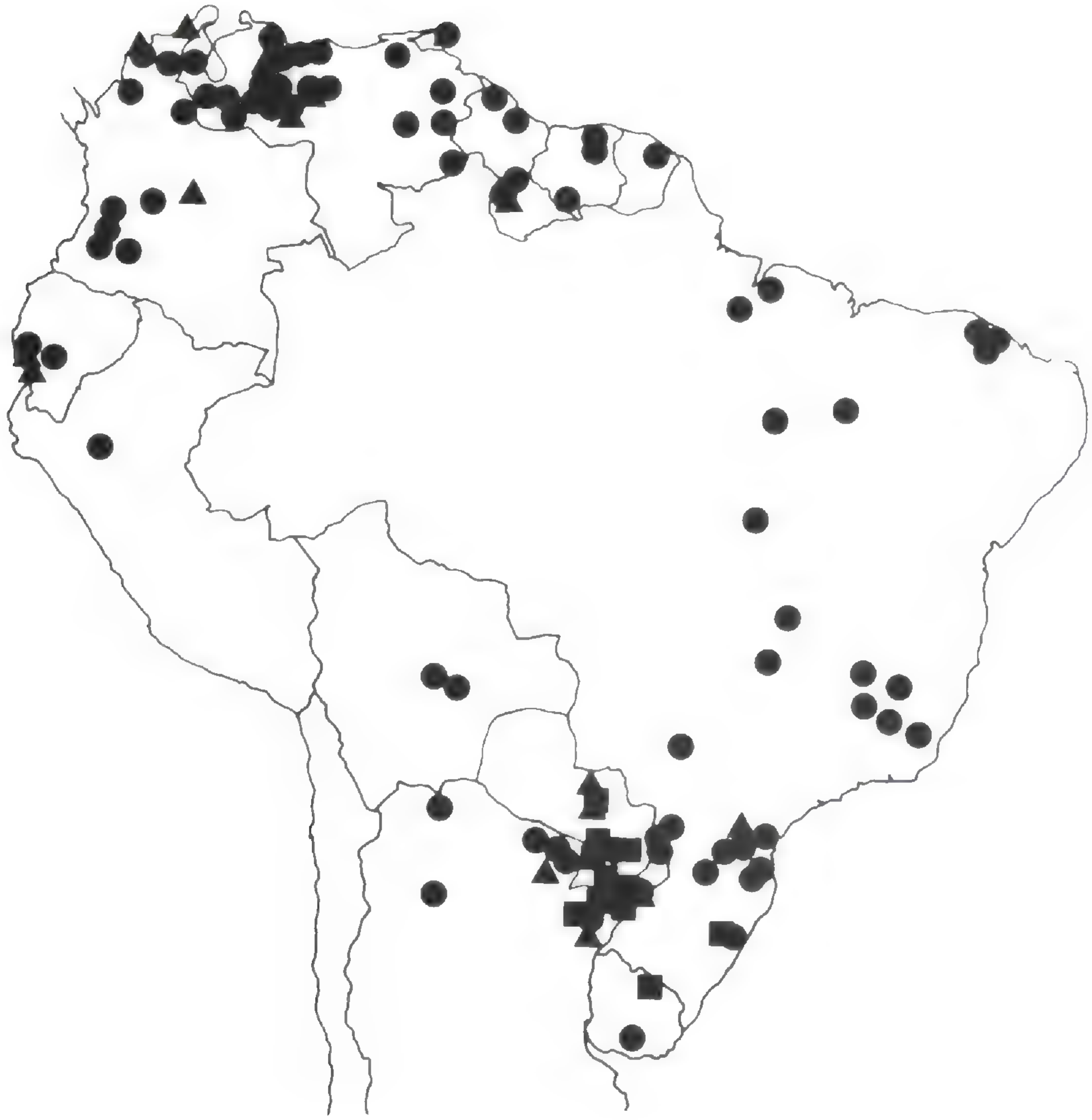


Figure 3. Distributions of *Hydrolea spinosa* var. *spinosa* (●), *H. spinosa* var. *paraguayensis* (■), and *H. elatior* (▲) in South America.

fluminis Y-aca, Jan 1900, *Hassler 6921* (G; ISOSYNTYPES: BM!, UC!; photographs of isosyntypes: UNA!); PARAGUAY, in stagnis pr. Arroyo Primero (Apa), Feb 1902, *Hassler 8485* (G; ISOSYNTYPES: BM!, UC!; photographs of syntype: UNA!; photographs of isosyntypes: UNA!).

Hydrolea paraguayensis var. *inermis* Chodat & Hassler, Bull. Herb. Boissier (ser. 2) 4:64. 1903. HOLOTYPE: PARAGUAY, ad marginem paludis in valle fluminis Y-aca, Jan 1900, *Hassler 6921a* (BM! [marked "Unicum"]; photographs of holotype: UNA!).

Herbs or small shrubs, to 8 dm tall, erect, usually broadly branched. Stems green or brown, hispid-hirsute. Leaves ovate to lanceolate, 2–12 cm long, 10–30 mm wide, densely pubescent to hispid-hirsute, with glandular trichomes; margins entire or serrulate. Thorns 1 per node, often absent, 4–25 mm long, 0.5–1.5 mm

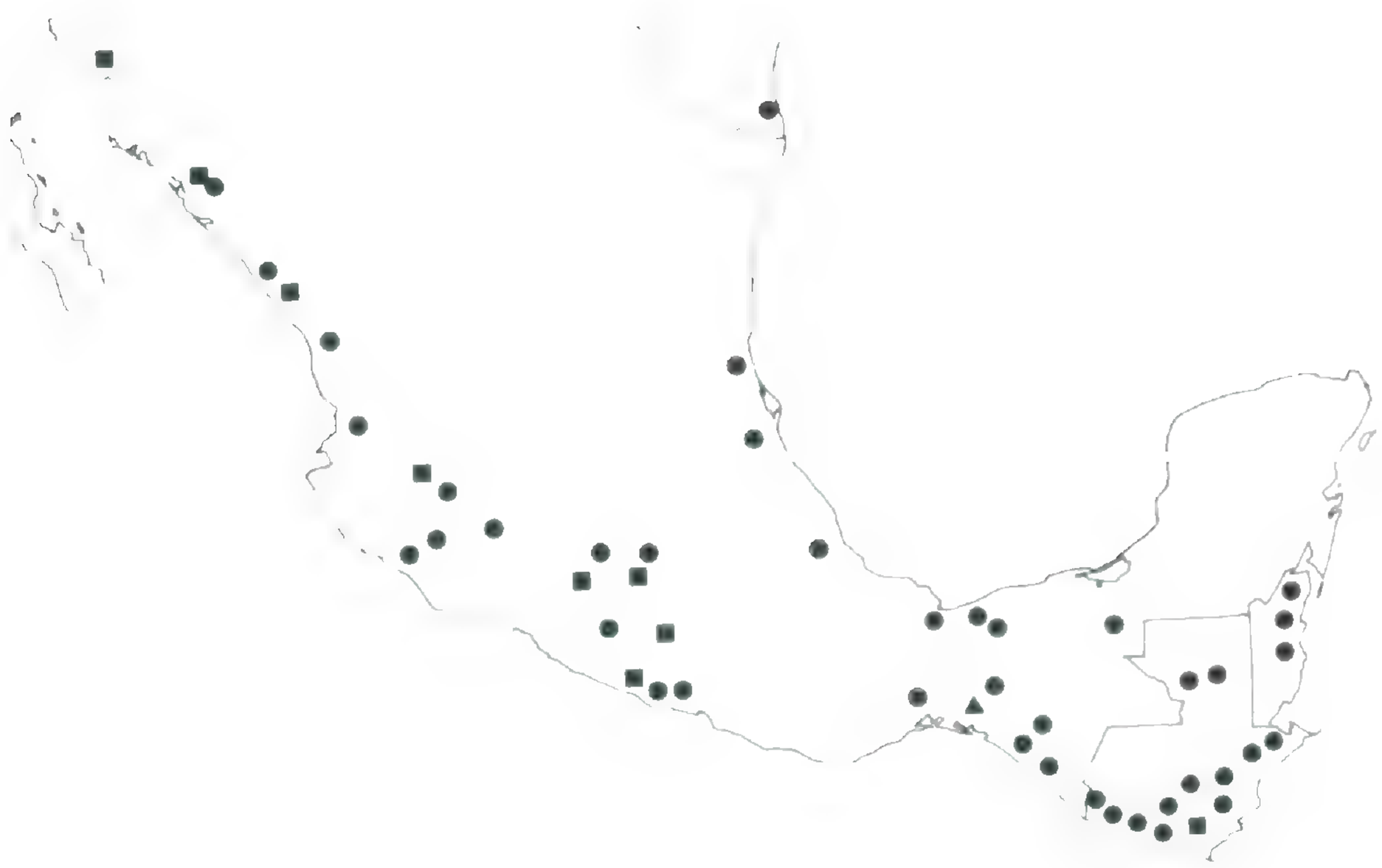


Figure 4. Distributions of *Hydrolea spinosa* var. *spinosa* (●), *H. spinosa* var. *maior* (■), and *H. elatior* (▲) in northern Central America.

broad. Flowers borne in broadly spreading, occasionally narrow, panicles. Sepals lanceolate, 6.5 14 mm long, 1.5 3.5 mm wide, densely pubescent to hispid-hirsute. Petals 8 17 mm long, 8–12 mm wide. Styles 2–3, 10–13 mm long. Capsule globose to ovoid, 4.5–8 mm long, 3.5–7 mm broad. Seeds cylindrical, 0.6–0.7 mm long; reticulations uniformly narrow.

DISTRIBUTION. Restricted to the Río Paraguay-Río Paraná basin of Paraguay and Argentina, and neighboring parts of Brasil and Uruguay. Flowering December to March. Figure 3.

DISCUSSION. This variety is marked by its large flowers, fruits and sepals and the dense (and often long) pubescence of the stems, leaves and sepals. The epithet "inermis" would have priority in the naming of this variety, due to the publication by Chodat & Hassler (1903) of *Hydrolea paraguayensis* var. *inermis*. However, *H. spinosa* var. *inermis* Spruce ex Bennett was previously and validly published (Bennett, 1871a), and the transfer of Chodat & Hassler's variety to *H. spinosa* would create a homonym. The epithet "megapotamica" cannot be used, because Brand (1913) published the combination *H. spinosa* var. *megapotamica* (Sprengel) Brand; this is an illegitimate name, because the validly published *H. spinosa* var. *inermis* was listed as a synonym. It becomes necessary, then, to transfer Macbride's epithet in naming this taxon.

Figure 5. Distributions of *Hydrolea spinosa* var. *spinosa* (●) and H. elatior (■) in southern Central America.

1c. **Hydrolea spinosa** var. **maior** (Brand) Davenport, *comb. nov.*
Hydrolea cervantesii var. *maior* Brand, Pflanzenr. 4, 251:184. 1913. HOLOTYPE: MEXICO, Michoacán or Guerrero, El Ocote, 12 Nov 1898, *Langlassé 619* (G; ISOTYPES: GH!, US!; photographs of holotype: UNA!; photographs of isotypes: UNA!).

Hydrolea cervantesii Brand, Pflanzenr. 4, 251:184. 1913. TYPE: Not seen; possibly with other Cervantes material at B, BR, MA or MEXU (Lanjouw & Stafleu, 1954).

Hydrolea angustifolia Cervantes ex Brand, Pflanzenr. 4, 251:184. 1913 (pro syn. sub *H. cervantesii*).

Herbs, to 6 dm tall, erect, unbranched. Stems green to brown, puberulent to densely pubescent. Leaves narrowly lanceolate to linear, 1.5–10 cm long, 2 15 mm wide, puberulent, with scattered hairs and glandular trichomes along veins and petioles; margins entire, often undulate. Thorns 1–2 per node, 5–20 mm long, 0.4–0.8 mm broad. Flowers borne in leafy panicles, often tightly clustered at branch tips. Sepals lanceolate, 5 9 mm long, 1 2.2 mm wide, puberulent to hispid-hirsute. Petals 5–8 mm long, 2 3.5 mm wide. Styles 2–3, 1.5–2.5 mm long. Capsule ovoid, 4.5–6 mm long, 3–4 mm

broad. Seeds cylindrical, 0.4–0.5 mm long; reticulations narrowing at the joints, the joints with papules.

DISTRIBUTION. Restricted to the Pacific slope of Mexico and Guatemala. Flowering October to March. Figure 4.

DISCUSSION. This variety differs from the typical variety in having smaller flower parts, narrower sepals, and narrower, undulate-margined leaves. In many specimens the flowers are borne in tight clusters at the branch tips. As is the case with var. *paraguayensis*, individuals of var. *maior* occupy one extreme of the distribution of var. *spinosa* and may be only recently isolated from that variety.

2. **Hydrolea elatior** Schott in Sprengel, Syst. veg. ed. 17, 4:404. 1827. HOLOTYPE: Without collection data or date, *Schott 34* (B [presumably destroyed]; marked "Original" by Brand; photographs of holotype: F!, GH!, UC!).

Hydrolea exaltata Schott ex Steudel, Nomencl. ed. 2, 1:782. 1840 (pro syn. sub *H. elatior*).

Hydrolea multiflora Martius ex Choisy, Prodr. 10:180. 1846. HOLOTYPE: [BRASIL, Matto Grosso,] Cujaba [Cuiabá], without date, *Martius 1248* (M; ISOTYPES: B [now destroyed], BM!, K, NY!; photographs of holotype: UNA!; photographs of isotypes: F!, GH!, NY!, UC!, UNA!).

Hydrolea multiflora β glabra Choisy, Prodr. 10:180. 1846. TYPE: Not seen; probably at G or G-DC (Stafleu & Cowan, 1976).

Nama multiflora (Martius ex Choisy) Kuntze, Revis. gen. pl. 2:435. 1891.

Hydrolea glabra var. *spinosa* Chodat & Hassler, Bull. Herb. Boissier (ser. 2) 4:64. 1903. SYNTYPES: PARAGUAY, in regione cursus superioris fluminis Apa, Dec 1901, *Hassler 8159* (G; ISOSYNTYPES: B [now destroyed], UC!; photographs of syntype: F!, UNA!; photograph of isosyntype: UC!); PARAGUAY, in campo humido pr. Bellavista, Apa, Nov 1901, *Hassler 7981* (G?).

Hydrolea glabra var. *spinosa* f. *albiflora* Chodat & Hassler, Bull. Herb. Boissier (ser. 2) 4:64. 1903. HOLOTYPE: PARAGUAY, in regione superioris fluminis Apa, Dec 1901, *Hassler 8159a* (G).

Hydrolea albiflora (Chodat & Hassler) Brand, Pflanzenr. 4, 251:182. 1913.

Hydrolea albiflora var. *depressa* Brand, Pflanzenr. 4, 251:183. 1913. HOLOTYPE: PARAGUAY, [Caaguazú,] prope Caaguazú, Feb 1905, *Hassler 8931* (G; ISOTYPE: BM!; photographs of holotype: UNA!; photographs of isotype: UNA!).

Hydrolea elatior var. *hirsutior* A. W. Bennett ex Brand, Pflanzenr. 4, 251:183. 1913. HOLOTYPE: [BRASIL, Distrito Federal,] Brasília, without date, *Sellow 938* (B [now destroyed]; photographs of holotype: F!, GH!, UC!).

Hydrolea cryptantha Brand, Pflanzenr. 4, 251:183. 1913. HOLOTYPE: [PARAGUAY,] Alto-Paraguay, Chaco, 1906, *Fiebrig 1318* (B [now destroyed]; ISOTYPE: G; photographs of holotype: F!, GH!, UC!; photographs of isotype: UNA!).

Hydrolea cryptantha var. *meridionalis* Hassler, Repert. Spec. Nov. Regni Veg. 13:238. 1914. HOLOTYPE: ARGENTINA, Chaco, Colonia Benítez, Dec (no year provided), *Stuckert 19556* (not seen).

Hydrolea minima Brand, Notizbl. Bot. Gart. Berlin-Dahlem 10:120. 1927. HOLOTYPE: [VENEZUELA,] Venezolanisches Guiana, Las Botellas, 3 Jan 1902, *Passarge & Selwyn 343* (B [now destroyed]; photographs of holotype: F!, GH!, UC!); PARATYPE: [VENEZUELA,] Venezolanisches Guiana, Tigrito, auf Sandboden, 19 Jan 1902, *Passarge & Selwyn 512* (B [now destroyed]).
Hydrolea glabra auct. non Schumacher: Bennett, Fl. bras. 7:396. 1871.

Herbs, to 6 dm tall, erect or prostrate, usually profusely branched and spreading. Stems green to brown, often purple, glabrous to densely pubescent, with or without glandular trichomes. Leaves ovate to lanceolate, 1.5–11 cm long, 3–20 mm wide, glabrous to puberulent, with or without glandular trichomes; margins entire to serrulate, often undulate; apices acute; bases attenuate to acute. Thorns absent. Flowers borne in broadly spreading panicles. Sepals lanceolate, 3.5–6 mm long, 1–2 mm wide, glabrous to puberulent, with or without glandular trichomes. Corolla blue, rarely white, the petals 3.5–8 mm long, 1.5–4 mm wide. Ovary glabrous to puberulent, the upper half often with glandular trichomes; styles 2, 1.5–4 mm long, glabrous. Capsule globose, 3–5 mm long, 2.5–5 mm wide, the upper half glabrous, puberulent or glandular-pubescent. Seeds broadly cylindrical, symmetrical, 0.4–0.5 mm long, 0.2–0.3 mm broad, with longitudinal ridges; reticulations uniformly broad. Chromosome number unknown.

DISTRIBUTION. Widely distributed in South America, with disjunct populations in Mexico and Honduras. Flowering October to June. Figures 4–5.

DISCUSSION. *Hydrolea elatior* is distinct among Western Hemisphere species because of its small flowers and fruits, lack of thorns, and often glabrous stems, leaves and sepals. Due to this glabrous condition, the species has at times been treated under *H. glabra* Schumacher [*H. palustris*].

Two growth forms are apparent in this species, resulting in nomenclatural confusion. Some profusely branched and spreading plants grow low to the ground, never reaching more than 1 dm in height. Many plants from northern South America exhibit this growth habit, and prompted Brand (1927) to describe *Hydrolea minima*. In contrast, in the Río de la Plata drainage system most plants of this species are tall, with numerous large stem leaves and terminal, spreading inflorescences. The low-growing forms are occasionally found in this region as well.

3. **Hydrolea nigricaulis** Wright ex Grisebach, Cat. pl. Cuba 207. 1866. HOLOTYPE: CUBA, without locality data, 1865, *Wright*

3108 (GOET; ISOTYPES: G, GOET, MO!, NY!, P, UC!, US!; photographs of holotype: UNA!; photographs of isotypes: UNA!).

Nama nigricaulis (Wright ex Grisebach) Kuntze, Revis. gen. pl. 2:435. 1891.

Herbs, to 5 dm tall, erect or decumbent, unbranched to broadly branched. Stems brown to black, puberulent to pubescent, without glandular trichomes. Leaves lanceolate to oblanceolate, 1 4 cm long, 3 10 mm wide, glabrous, puberulent or gland-dotted; margins entire or serrulate, often undulate; apices acute; bases attenuate to acute. Thorns usually present, 1 per node, 4–11 mm long, 0.3–0.8 mm broad. Flowers borne in axillary fascicles, 1 4 per fascicle. Sepals lanceolate, 2.5–4.5 mm long, 0.4–1 mm wide, glabrous to puberulent, often with short, stout hairs. Corolla white, the petals 2.5 4 mm long, 0.5 1.5 mm wide. Ovary glabrous; styles 2 3, 0.6–1 mm long, glabrous. Capsule globose to ovoid, 2–3.5 mm long, 1.5–3 mm wide, glabrous. Seeds cylindrical, often asymmetrical, 0.3–0.4 mm long, 0.1–0.2 mm wide, with longitudinal ridges; reticulations uniformly broad. Chromosome number unknown.

DISTRIBUTION. Restricted to Cuba and Jamaica. Flowering year-round. Figure 6.

DISCUSSION. *Hydrolea nigricaulis,* with its axillary fascicles of small, white flowers, is unlike any other species in the genus. Only *H. elatior* has flower parts and capsules of a similar small size, and no other species has uniformly white flowers. The capsules are often 3-loculed and ovoid; the upper leaf surfaces may be covered by round glands.

Two growth forms can be distinguished in *Hydrolea nigricaulis.* Erect plants are marked by prolific side branches, each with many flower clusters; prostrate plants have fewer side branches bearing fewer flower clusters.

4. **Hydrolea corymbosa** Macbride ex Elliott, Sketch bot. S. Carolina 336. 1817. HOLOTYPE: [UNITED STATES,] South Carolina, in stagnis St. Stephens, without date, *Macbride s. n.* (CHARL; ISOTYPE: K; photographs of holotype: GH!, NY!; photographs of isotype: UNA!).

Nama corymbosa (Macbride ex Elliott) Kuntze, Revis. gen. pl. 2:435. 1891.

Herbs, to 6 dm tall, erect, unbranched or with short reproductive branches. Stems green, brown or purple, densely pubescent, without glandular trichomes. Leaves lanceolate, 20–55 mm long, 3–10 mm

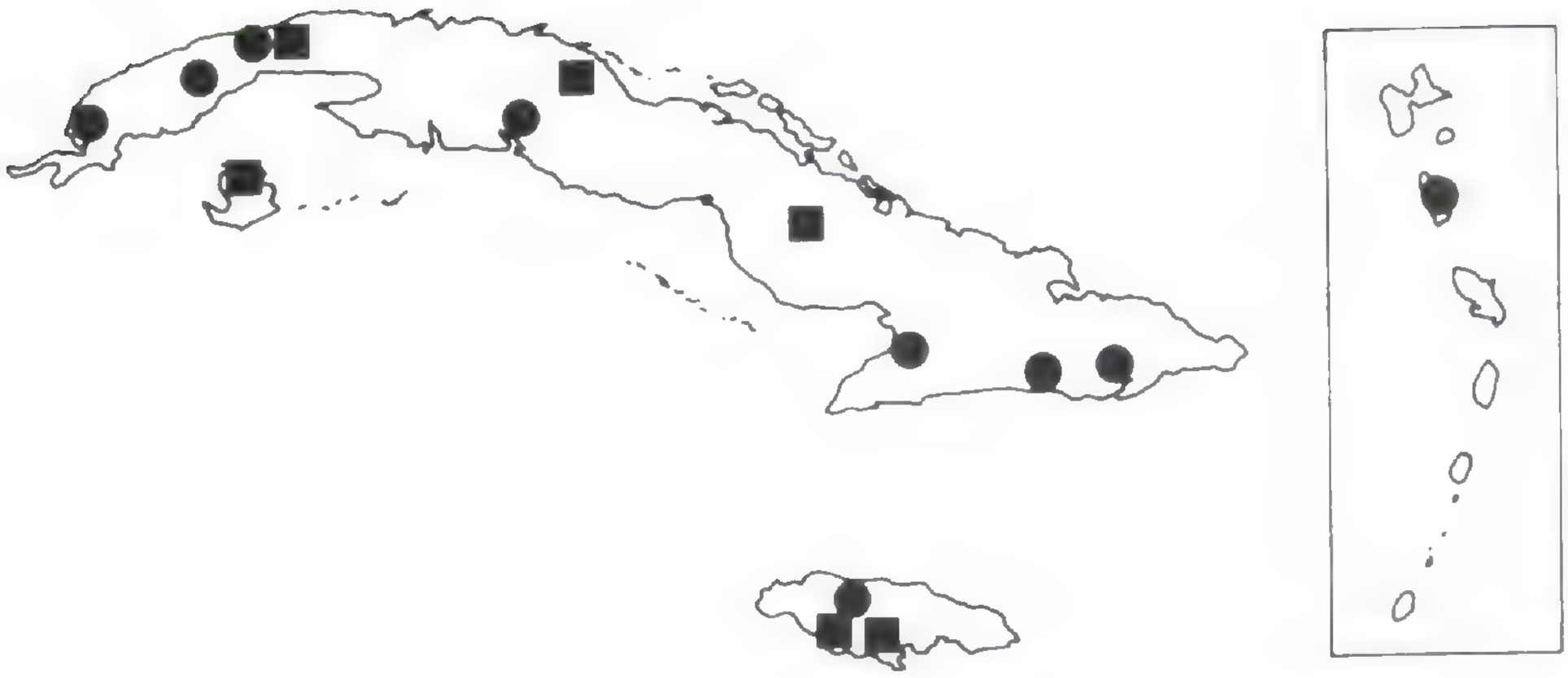


Figure 6. Distributions of *Hydrolea spinosa* var. *spinosa* (●) and *H. nigricaulis* (■) in the Caribbean.

wide, glabrous to puberulent; margins serrulate; apices acuminate to acute; bases acute to rounded. Thorns rare, 1 per node or absent, 4–11 mm long, 0.2–0.6 mm broad. Flowers borne in leafy panicles or corymbs. Sepals lanceolate, 4.5–7 mm long, 1–2 mm wide, hispid-hirsute, with glandular trichomes. Corolla blue, the petals 10 15 mm long, 5–8 mm wide. Ovary glabrous to puberulent, the upper half often with glandular trichomes; styles 2, 5–10 mm long, glandular-pubescent toward bases. Capsule globose to slightly ovoid, 3–4.5 mm long, 2.5–4 mm wide, the upper half puberulent or glandular-pubescent. Seeds broadly ovoid, symmetrical, 0.6–0.7 mm long, 0.3–0.4 mm wide, with longitudinal and latitudinal ridges; reticulations narrowing at the joints, the joints with papules. Chromosome number unknown.

DISTRIBUTION. Restricted to the coastal plain of the southeastern United States; widespread in Florida and southern Georgia, and known from two counties of South Carolina. Flowering July to September. Figure 7.

DISCUSSION. *Hydrolea corymbosa* has the most restricted distribution of any of the North American species, being found only in Florida, Georgia and South Carolina. This species is morphologically very similar to the more western *Hydrolea ovata*, sharing the paniculate or corymbose type of inflorescence and similar stem and sepal pubescence. *Hydrolea corymbosa*, however, is a much smaller and more slender plant with fewer (if any) thorns, stems that are dark brown or purple, and nearly glabrous, lanceolate leaves with rounded bases. A combination of these characters will easily separate the two species.

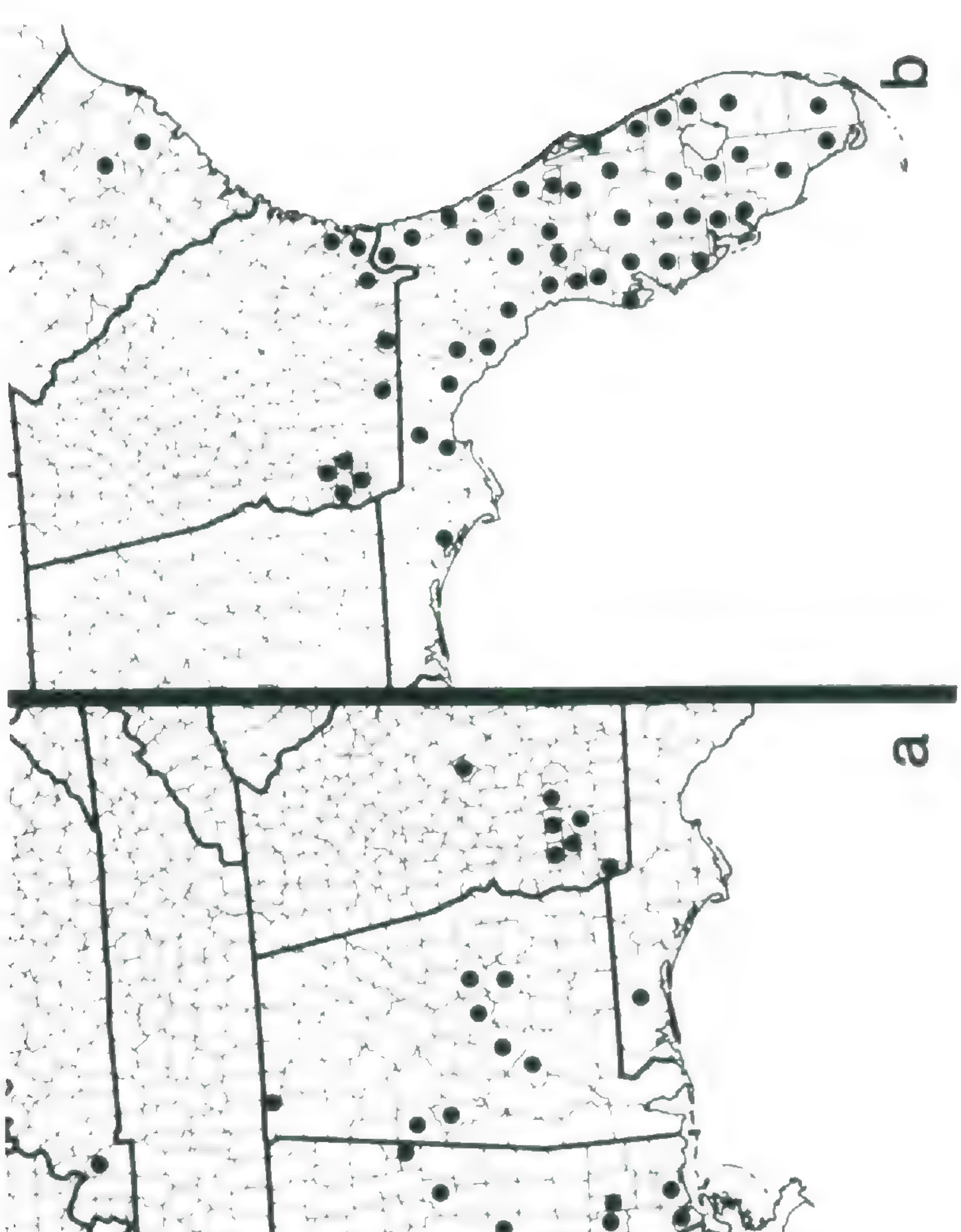


Figure 7. Distributions of *Hydrolea ovata* (a) and *H. corymbosa* (b) in the United States.

Although the type specimen was collected in South Carolina, Radford et al. (1968) omitted the species from their treatment of Carolina plants. The type—still at CHARL (A. E. Sanders, pers. comm.) was also omitted by Weatherby (1942) from his documentation of the Elliott herbarium.

5. **Hydrolea ovata** Nuttall ex Choisy, Mém. Soc. Phys. Genève 6:109. 1833. TYPE: [UNITED STATES,] hab. in Akansa [Arkansas], without date or collector (G-DC?). The type collection was not found at G-DC, although Choisy indicated that as its location. The excellent illustration accompanying the original description, however, is unmistakably of this species.

Hydrolea ovatifolia Raf., New fl. No. Amer. pt. 4:64. 1836. TYPE: Not seen and probably destroyed (see Stuckey, 1971).

Hydrolea paniculata Raf., New fl. No. Amer. pt. 4:64. 1836. TYPE: Not seen and probably destroyed (see Stuckey, 1971).

Hydrolea ovata Nuttall, Trans. Amer. Philos. Soc. (new ser.) 5:196. 1836. LECTOTYPE (here designated): [UNITED STATES,] Arkansa[s], without collection data or date, *Nuttall s. n.* (BM!; ISOLECTOTYPE: K; photographs of lectotype: UNA!; photographs of isolectotype: UNA!).

Nama ovata (Nuttall ex Choisy) Britton, Mem. Torrey Bot. Club 5:272. 1894.

Hydrolea ovata var. *georgiana* Brand, Pflanzenr. 4, 251:180. 1913. LECTOTYPE (here designated): [UNITED STATES,] Georgia, Mitchell Co., shallow water in the "Slough" near Camilla, 8 Aug 1901, *Harper 1170* (BM!; ISOLECTOTYPE: MO!; photographs of lectotype: UNA!; photographs of isolectotype: UNA!).

Hydrolea spinosa auct. non L.: Torrey, Ann. Lyceum Nat. Hist. New York 2:223. 1828.

Herbs or small shrubs, to 1 m tall, erect, usually broadly branched. Stems green to brown, densely pubescent, occasionally with a few longer or glandular trichomes. Leaves ovate, occasionally orbicular, 1.5–7 cm long, 10–25 mm wide, pubescent; margins entire, often undulate; apices acuminate to acute; bases attenuate, acute or obtuse. Thorns 1–2 per node, 5–12 mm long, 0.3–0.8 mm broad. Flowers borne in broadly branching panicles. Sepals narrowly lanceolate, 6–9 mm long, 1–2.5 mm wide, hispid-hirsute, with glandular trichomes. Corolla blue, occasionally white, the petals 11–17 mm long, 5–9 mm wide. Ovary glabrous to puberulent, the upper half often with glandular trichomes; styles 2, 10–15 mm long, glandular-pubescent toward bases. Capsule globose, 4.5–5.5 mm long, 4–5.5 mm wide, the upper half puberulent or glandular-pubescent. Seeds cylindrical, symmetrical, 0.5–0.6 mm long, 0.2–0.3 mm wide, with longitudinal ridges; reticulations narrowing at the joints, the joints with papules. Chromosome number: $2n = 20$ (Constance, 1963).

DISTRIBUTION. Widespread in the south-central United States, from eastern Texas and Oklahoma east to southwestern Georgia, north to southern Missouri and Kentucky. Flowering July to September. Figure 7.

DISCUSSION. As discussed previously, *Hydrolea ovata* and *H. corymbosa* share a number of characteristics. *Hydrolea ovata* is much more robust, with densely pubescent stems and leaves. The leaves are ovate, while those of *H. corymbosa* are lanceolate.

Hydrolea ovata shares characteristics with *H. spinosa* as well. Some forms of *H. spinosa* have small, rounded leaves similar to those of *H. ovata*; these forms were recently described by Nash (1979) as *H. ovata* var. *parvifolia*. The stems of *H. ovata*, however, are only rarely glandular-pubescent and the styles are much longer that those found in *H. spinosa*.

Although reported from Brasil (Bennett, 1871b), *Hydrolea ovata* is one of four species restricted to the United States. It has the most westerly distribution of any of the four, being most frequently encountered in Texas, Louisiana, Oklahoma, and Arkansas.

6. **Hydrolea uniflora** Raf., Autikon Bot. 24. 1840. TYPE: Not seen and probably destroyed (see Stuckey, 1971). The type description is unmistakably of this species.

Hydrolea affinis Gray, Manual ed. 5, 370. 1867. TYPE: Not seen; possibly at GH (Stafleu & Cowan, 1976).

Nama affinis (Gray) Kuntze, Revis. gen. pl. 2:435. 1891.

Herbs, to 6 dm tall, erect or decumbent, unbranched, with short reproductive branches or with branches arising from prostrate stems. Stems green to brown, glabrous to puberulent, without glandular trichomes. Leaves lanceolate, 3 10 cm long, 10 20 mm wide, glabrous; margins entire or serrulate, often undulate; apices acuminate to acute; bases attenuate to acute. Thorns 1–2 per node, 6–15 mm long, 0.5 1.2 mm broad. Flowers borne in axillary fascicles, 1 10 per fascicle, or on short, leafy branches. Sepals broadly lanceolate to ovate, 5 8 mm long, 1.5 4 mm wide, glabrous to puberulent, without glandular trichomes. Corolla blue, occasionally white, the petals 7-11 mm long, 4-6 mm wide. Ovary glabrous; styles 2, 3.5–5 mm long, glabrous. Capsule globose, 4.5 7 mm long, 4.5 7 mm wide, glabrous. Seeds ovoid, 0.5 0.6 mm long, 0.2 0.3 mm wide, with longitudinal ridges; reticulations narrowing at the joints, the joints with papules. Chromosome number: $2n = 20$ (Constance, 1963).

DISTRIBUTION. Widespread in the lower Mississippi Valley of North America, from eastern Texas and Oklahoma east to western Alabama, from southern Louisiana north to southern Illinois. Flowering June to September. Figure 8.

DISCUSSION. *Hydrolea uniflora* is very similar morphologically to *H. quadrivalvis*, but differs from the latter in its lacking long, jointed hairs and by having flower clusters borne on long (up to 4 cm) peduncles. The favored name for this species has historically been *Hydrolea affinis* Gray. However, as Fernald (1944) pointed out, Rafinesque's description of the species is unmistakable and predates Gray's by nearly 30 years. It is difficult, if not impossible, to locate a type specimen for this species, since Rafinesque's collections were destroyed or scattered following his death (Stuckey, 1971).

Hydrolea ovata × *uniflora*

A number of specimens collected in Louisiana and eastern Texas appear to result from hybridization between *Hydrolea ovata* and *H. uniflora*. Although noted on herbarium sheets by earlier workers, the occurrence of these hybrids was first published by Correll & Johnston (1970).

Hybrids are marked by several characteristics intermediate between the two species. Leaves are ovate-lanceolate and sparsely pubescent. Stems and sepals are also pubescent, with the latter sometimes glandular-pubescent; the dense, hispid-hirsute pubescence of *Hydrolea ovata* sepals, however, is rarely seen. Petals are either the same size as in one of the species or intermediate. Hybrids are generally extensively branched, with branches from the lower nodes producing a much bushier and more sprawling plant than is typical of either species. Clusters of flowers are borne either at the tips or at the nodes of these lateral branches.

7. **Hydrolea quadrivalvis** Walter, Fl. car. 109. 1788. TYPE: Not located; apparently not with Walter's material at BM (A. O. Chater, pers. comm.).

Hydrolea caroliniana Michaux, Fl. bor.-amer. 1:177. 1803 (nom. superfl., because *H. quadrivalvis* was listed in synonymy).
Nama caroliniana (Michaux) Kuntze, Revis. gen. pl. 2:435. 1891.
Nama quadrivalvis (Walter) Kuntze, Revis. gen. pl. 2:435. 1891.
Hydrolea opercularia Willd. ex Brand, Pflanzenr. 4, 251:183. 1913 (pro syn. sub *H. quadrivalvis*).

Herbs, to 6 dm tall, erect or decumbent, unbranched, with short reproductive branches or with branches arising from prostrate

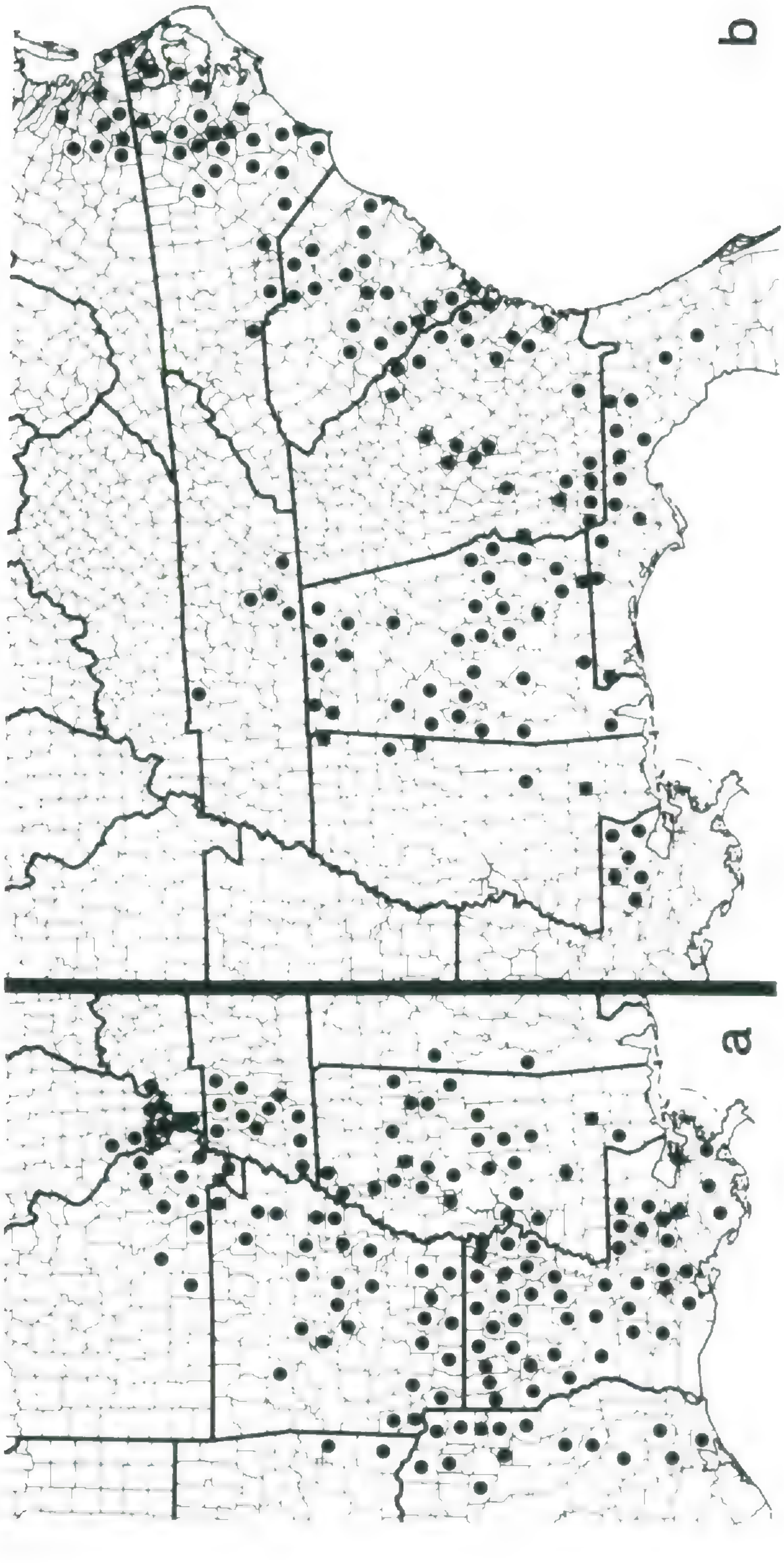


Figure 8. Distributions of *Hydrolea uniflora* (a) and *H. quadrivalvis* (b) in the United States.

stems. Stems green to brown, with long, jointed hairs. Leaves lanceolate, 4–10 cm long, 10–25 mm wide, with occasional long trichomes restricted to veins; margins entire or serrulate, often undulate; apices acuminate to acute; bases attenuate to acute. Thorns 1–2 per node, rarely absent, 5–12 mm long, 0.6–1.2 mm broad. Flowers borne in axillary fascicles, 1–10 per fascicle, or on short, leafy branches. Sepals lanceolate, 6–10 mm long, 1.5–2.5 mm wide, bearing long, jointed hairs. Corolla blue, rarely white, the petals 8–11 mm long, 3.5–6 mm wide. Ovary glabrous; styles 2, 3.5–5 mm long, glabrous. Capsule globose, 5.5–7 mm long, 5–7 mm wide, glabrous. Seeds cylindrical, 0.6–0.7 mm long, 0.2–0.3 mm wide, with longitudinal ridges; reticulations narrowing at the joint, the joints with papules. Chromosome number: $2n = 20$ (Cave & Constance, 1959; Constance, 1963).

DISTRIBUTION. Widespread in the coastal plain of the southeastern United States, from southeastern Louisiana east to middle Florida, north to southern Tennessee and eastern Virginia. Flowering July to September. Figure 8.

DISCUSSION. In gross morphology, *Hydrolea quadrivalvis* is closest to *H. uniflora* and *H. palustris*. It differs from these two species in having long, jointed hairs on stems and sepals. Flower clusters are borne on peduncles longer than those of *H. palustris* but far shorter than those of *H. uniflora*.

Hydrolea quadrivalvis is commonly found bordering waterways of the Atlantic and Gulf coastal plains of North America. Recently it has also been collected in the Tennessee Valley (Van Horn, 1981) and in northwestern Tennessee (Chester, 1970).

Hydrolea section **Attaleria** (Poiret) Brand, Pflanzenr. 4, 251: 174. 1913.

*Attalé*rie Poiret, Encycl., Suppl. 1:535. 1811.

Herbs, to 8 dm tall. Stems green to brown, often tinged with purple, glabrous to densely pubescent, occasionally with glandular trichomes. Leaves ovate, lanceolate or linear, 2–12 cm long, 2–25 mm wide, glabrous to puberulent, without glandular trichomes; margins entire, often undulate; apices acuminate to acute, occasionally rounded; bases attenuate, acute, rounded or cordate-clasping. Thorns absent. Flowers borne in terminal corymbs, leafy panicles, short-pedunculate (<1 cm long) axillary fascicles, or singly in leaf axils. Sepals lanceolate to cordate, 4–8 mm long, 1–7.5 mm wide,

glabrous to densely pubescent, occasionally with glandular trichomes. Corolla blue, the petals 3.5–10 mm long, 1.5–3.5 mm wide. Ovary glabrous, or the upper half puberulent; placentas entire in cross-section; styles 2 3, 0.8–5.5 mm long, glabrous. Capsule globose, subglobose or cylindrical, occasionally truncated at style bases, erect or drooping at maturity, 2.5–5.5 mm long, 2–4.5 mm broad, glabrous or the upper half puberulent. Seeds ovoid to cylindrical, symmetrical, 0.3 0.6 mm long, 0.2 0.3 mm broad, with longitudinal and (in 1 species) transverse ridges; reticulations uniformly broad or narrowing at the joints, the joints without papules, with or without circles or half-circles. Chromosome number: $n = 9, 12$. LECTOTYPE SPECIES: *H. zeylanica* (L.) Vahl. (Lectotype here designated.)

KEY TO SPECIES OF *HYDROLEA* SECTION *ATTALERIA*

1. Flowers borne in axillary fascicles ..... **9.** *H. palustris*
1. Flowers borne in terminal corymbs or leafy panicles 2
2. Sepals cordate; leaf bases obtuse to cordate-clasping .... **11.** *H. macrosepala*
2. Sepals lanceolate; leaf bases acute to attenuate 3
3. Leaves linear, straplike ..... **10.** *H. floribunda*
3. Leaves ovate to lanceolate, not straplike .... **8.** *H. zeylanica*

8. **Hydrolea zeylanica** (L.) Vahl, Symb. bot. 46. 1791. *Nama zeylanica* L., Sp. pl. 226. 1753 ("Zaylanica"). LECTOTYPE (here designated): Without collection data, date or collector (LINN; IDC 144:322.1).

Steris javana L., Mant. pl. 54. 1767. LECTOTYPE (here designated): Without collection data, date or collector (LINN; IDC 144: 322.2).

Steris aquatica N. L. Burman, Fl. indica 73. 1768. TYPE: Not seen; possibly at G, L, LINN, M or UPS (Stafleu & Cowan, 1976).

Hydrolea inermis Loureiro, Fl. cochinch. 172. 1790. LECTOTYPE (here designated): Without collection data or date, in Loureiro collection (P; photographs of lectotype: F!, UNA!).

Hydrolea javanica Blume, Bijdr. fl. Ned. Ind. 725. 1826. TYPE: Not seen; possibly at BO, L or P (Stafleu & Cowan, 1976).

Hydrolea arayatensis Blanco, Fl. Filip. 211. 1837. TYPE: Not seen; if extant, probably at G or MA (Stafleu & Cowan, 1976).

Reichelia palustris Blanco, Fl. Filip. 220. 1837. TYPE: Not seen; if extant, probably at G or MA (Stafleu & Cowan, 1976).

Beloanthera oppositifolia Hasskarl, Flora 25:55. 1842. TYPE: Not seen; possibly at L (Stafleu & Cowan, 1979).

Hydrolea zeylanica β ciliata Choisy, Prodr. 10:180. 1846. TYPE: Not seen; probably at G or G-DC (Stafleu & Cowan, 1976).
Hydrolea ceilonica F. von Mueller, Fragm. 5:192. 1866 (orth. var.).
Hydrolea sansibarica Gilg, Pflanzenw. Ost-Afrikas 5:335. 1895. SYNTYPES: [TANZANIA,] Usambara, Muoa [Mlola], Jul 1893, *Holst 3105* (B [now destroyed]; ISOSYNTYPE: BM!; photographs of isosyntype: UNA!); ZANZIBAR, Tusel, Oct 1875, *Hildebrandt 994* (B [now destroyed]; ISOSYNTYPES: BM!, K, MO!; photographs of isosyntypes: UNA!); [ZANZIBAR,] Kokotoni [Mkokotoni], without date, *Stuhlmann 747* (B [now destroyed]; no isosyntypes located).
Hydrolea zeylanica var. *glabra* Brand, Pflanzenr. 4, 251:175. 1913. SYNTYPES: [SRI LANKA,] Ceylon, without date, *Thwaites 1883* (BM!, G[2]; photographs of isosyntypes: UNA!); INDIA, Madura, without date, *Meebold s. n.* (not seen); [INDONESIA,] Java, without date, *Hoffmannsegg s. n.* (not seen).
Hydrolea prostrata Exell, J. Bot. 67, Suppl. 2:106. 1929. HOLOTYPE: ANGOLA: Quissama, in dried-up swamps at Candomba, Rio Longa, 2 Jun 1921, *Gossweiler 8278* (BM!; photographs of holotype: UNA!).
Hydrolea zeylanica var. *erecta* Haines, Bot. Bihar Orissa 572. 1922. TYPE: Not seen; possibly at K (Stafleu & Cowan, 1979).
Hydrolea zeylanica var. *diffusa* Haines, Bot. Bihar Orissa 572. 1922. TYPE: Not seen; possibly at K (Stafleu & Cowan, 1979).
Nama jamaicense auct. non L.: Blanco, Fl. Filip. 211. 1837 ("Jamaicensis").

Herbs, to 6 dm tall, erect or prostrate, unbranched to broadly branched. Stems green to brown, often tinged with purple, glabrous to densely pubescent, occasionally with glandular trichomes. Leaves ovate to lanceolate, 2–10 cm long, 3–25 mm wide, glabrous to puberulent; apices acuminate to acute, occasionally rounded; bases attenuate to acute. Flowers borne in narrow or broadly branching panicles or densely clustered at branch tips. Sepals lanceolate, 4.5–8 mm long, 1–2 mm wide, glabrous to densely pubescent, occasionally with glandular trichomes. Petals 5–8 mm long, 1.5–3.5 mm wide. Ovary glabrous, the upper half occasionally puberulent; styles 1–2.5 mm long. Capsule globose to cylindrical, occasionally truncated at style bases, usually erect at maturity, 4–5 mm long, 2.5–3.5 mm broad, the upper half glabrous to puberulent. Seeds ovoid, 0.3–0.4 mm long, with longitudinal and transverse ridges; reticulations narrowing at the joints, the joints with circles or half-circles. Chromosome number: $n = 9$ (Datta & Manna, 1963; Sarkar et al., 1973), $n = 12$ (Krishnappa, 1971).

DISTRIBUTION. Widely distributed in tropical Asia, from Africa to the Philippines and Australia. Flowering July to March. Figures 9–10.

DISCUSSION. *Hydrolea zeylanica* is by far the most widely distributed and morphologically variable species of this section. Both erect and prostrate forms occur—apparently due to ecological con-

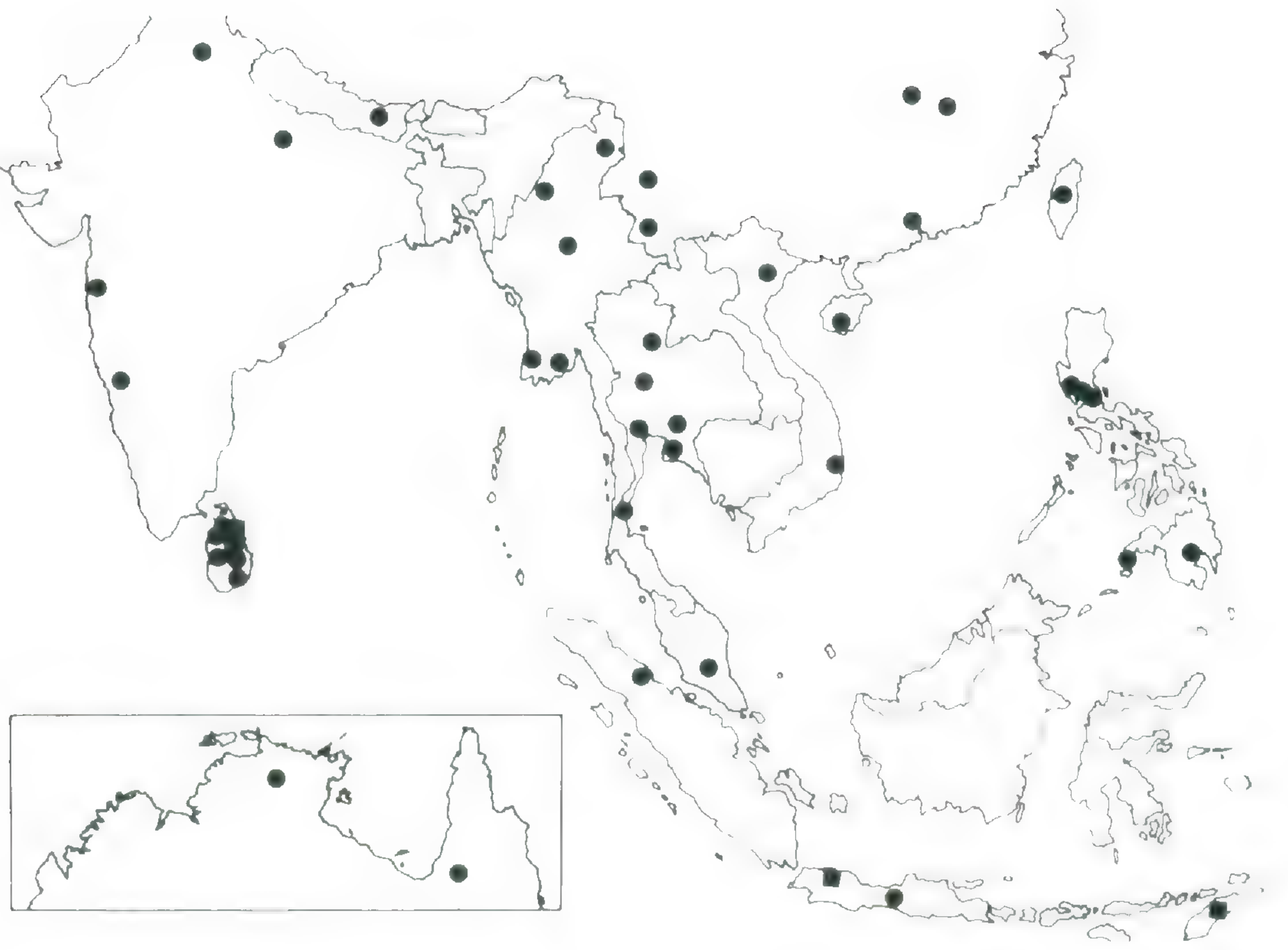


Figure 9. Distributions of *Hydrolea zeylanica* (●) and *H. spinosa* var. *spinosa* (■) in tropical Asia.

ditions (Merrill, 1918)--and many of the numerous synonyms are based on differences between these two forms. In erect plants the leaves are long and lanceolate, with the clusters of flowers at the branch tips often forming a broad, conical inflorescence. In prostrate plants the leaves are shorter and more rounded, with much narrower inflorescences arising from the rooted nodes. Banerji et al. (1974) also found differences between the two forms in the sizes of the flower parts and in the pubescence of the sepals.

Hydrolea zeylanica is most similar in gross morphology to the Western Hemisphere *H. elatior*. Individuals of *H. zeylanica*, however, are more often glabrous (especially along the stems), with longer, more cylindrical capsules, and acuminate sepals that far exceed the capsules in length.

9. **Hydrolea palustris** (Aublet) Raeuschel, Nomencl. ed. 3, 76. 1797. *Sagonea palustris* Aublet, Hist. pl. Guiane 1:285. 1775. LECTOTYPE (here designated): Without collection data or date, *Aublet s. n.* (P; ISOLECTOTYPE: BM!; photographs of lectotype: NY!, UNA!; photographs of isolectotype: UNA!).

Reichelia guianensis Sprengel, Syst. veg. ed. 17, 1:940. 1825 (nom. superfl., because *Sagonea palustris* was cited in synonymy).
Hydrolea glabra Schumacher, Beskr. Guin. plant. 181. 1827. LECTOTYPE (here designated): Guinea, without date or collector (C; IDC card 54).
Hydrolea quadrivalvis β inermis Choisy, Mém. Soc. Phys. Genève 6:109. 1833. HOLOTYPE: Without collection data or date, *Aublet s. n.* (BM!; photographs of holotype: UNA!).
Hydrolea bartramii Choisy, Mém. Soc. Phys. Genève 6:109. 1833 (pro syn. sub *H. quadrivalvis β inermis*).
Hydrolia madagascariensis Choisy, Mém. Soc. Phys. Genève 6:111. 1833. TYPE: Not seen; possibly at G or G-DC (Stafleu & Cowan, 1976).
Hydrolea guineensis Choisy, Ann. Sci. Nat. Bot. (ser. 2) 1:180. 1834 (nom. superfl., because *H. glabra* was cited in synonymy).
Nama glabra (Schumacher) Kuntze, Revis. gen. pl. 2:435. 1891.

Herbs, to 6 dm tall, erect or decumbent, with short reproductive branches or with branches arising from prostrate stems, or unbranched. Stems green to brown, glabrous. Leaves lanceolate, 4–12 cm long, 7–25 mm wide, glabrous; apices acuminate to acute; bases attenuate to acute. Flowers borne on short, leafy branches in axillary fascicles of 1–4, or singly in leaf axils. Sepals lanceolate, 5–7.5 mm long, 1.5–3 mm wide, glabrous, occasionally puberulent. Petals 5–7 mm long, 2–3 mm wide. Ovary glabrous; styles 1.5–2 mm long. Capsule globose, often drooping at maturity, 3.5–5.5 mm long, 3.5–4.5 mm broad, glabrous. Seeds ovoid, 0.4–0.6 mm long, with longitudinal ridges; reticulations narrowing at the joints, the joints with circles. Chromosome number unknown.

DISTRIBUTION. Restricted to tropical Africa. Flowering April to September. Figure 10.

DISCUSSION. *Hydrolea palustris* is the only species in this section with truly axillary inflorescences. The flowers may be solitary at the nodes of the main stem or borne in fascicles; in a few specimens the flowers are borne on short, leafy branchlets. Mature capsules often droop, which is a characteristic shared with *H. zeylanica* and *H. floribunda*.

Many different names have been applied to this species. Most authors have used the name *Hydrolea glabra*, following Schumacher's (1827) work on the plants of Guinea. The species, however, was first described by Aublet (1775) as the type of his genus *Sagonea*, from French Guiana. Schumacher's plant clearly matches Aublet's original drawing; seeds from African plants—with circles at the reticulation joints—also match those from the isolectotype of *S. palustris*.

The question remains as to how an African plant came to be described in a work on northern South America, and I submit two

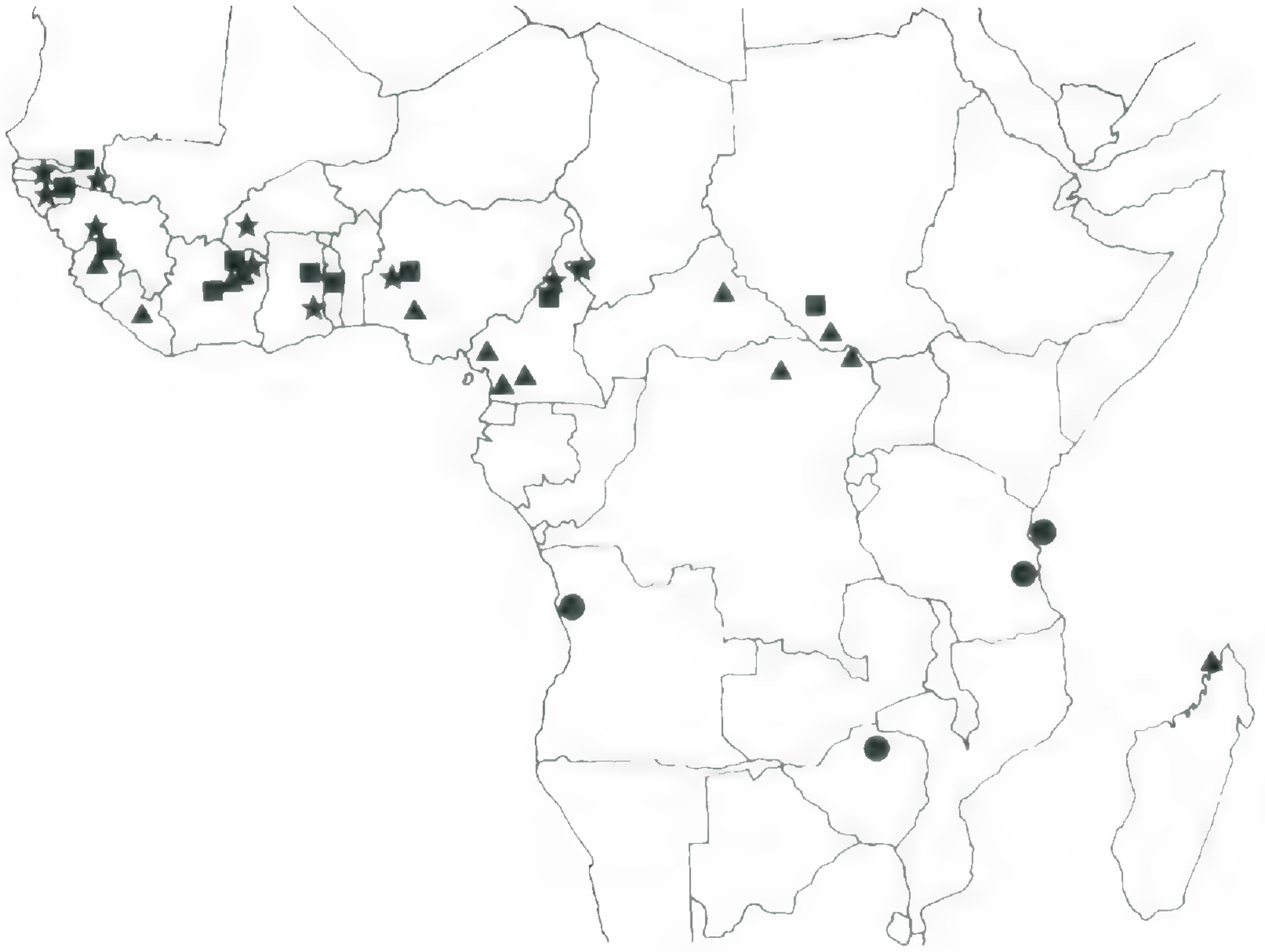


Figure 10. Distributions of *Hydrolea zeylanica* (●), *H. palustris* (▲), *H. floribunda* (■), and *H. macrosepala* (★) in Africa.

plausible explanations. The simplest explanation is that the names "Guinea" and "Guiana" became confused, with Aublet treating an African specimen as native to French Guiana. A second explanation is that the type specimen was actually collected in South America and represents a waif that failed to become established. Slave ships and other vessels crossing the Atlantic Ocean from western Africa to northern South America could have provided the means for such a dispersal.

10. **Hydrolea floribunda** Kotschy & Peyritsch, Pl. tinn. 22. 1867. HOLOTYPE: [SUDAN,] in aquaticis prope Bongo copiosissima, 1863, *Tinne 31* (W!; photographs of holotype: UNA!).

Hydrolea graminifolia A. W. Bennett, J. Linn. Soc., Bot. 11:277. 1871. HOLOTYPE: [NIGERIA, Kwara,] swamp near Jeba [Jebba], 1858, *Barter 888* (K; ISOTYPES: GH!, K, W!; photographs of holotype: UNA!; photographs of isotypes: UNA!).

Hydrolea floribunda (Kotschy & Peyritsch) Kuntze, Revis. gen. pl. 2:435. 1891.

Hydrolea barteri Peter, Nat. Pflanzenfam. 4, 3a:71. 1893 (nom. superfl., apparently referring to Barter's type collection of *H. graminifolia*).

Herbs, to 8 dm tall, erect, usually broadly branched. Stems green to brown, glabrous to puberulent. Leaves linear, 4–12 cm long, 2–5

mm wide, glabrous; apices acuminate; bases attenuate. Flowers borne in terminal, compound corymbs. Sepals lanceolate, 4 5.5 mm long, 1 1.5 mm wide, glabrous to puberulent. Petals 6–10 mm long, 2–3.5 mm wide. Ovary glabrous; styles 3.5–5.5 mm long. Capsule globose to slightly cylindrical, often drooping at maturity, 2.5–4 mm long, 2 3.5 mm broad, glabrous. Seeds cylindrical, 0.4 0.5 mm long, with longitudinal ridges; reticulations uniformly broad and closely overlapping. Chromosome number unknown.

DISTRIBUTION. Restricted to tropical Africa. Flowering year-round. Figure 10.

DISCUSSION. This is one of the most distinctive species of *Hydrolea*, characterized by long, linear leaves and broad, terminal inflorescences. The mature capsules droop in the same manner as those of *H. zeylanica* and *H. palustris*.

The type collection of *Hydrolea floribunda* was made during the ill-fated African expedition of three women named Tinne. This party set out to cross central Africa from Khartoum to Fernando Po, but was forced to turn back after much hardship and the deaths of two of the women. The type was probably collected near the headwaters of the Bahr el Ghazal in southern Sudan (see Gladstone, 1970).

11. **Hydrolea macrosepala** A. W. Bennett, J. Linn. Soc., Bot. 11:277. 1871. HOLOTYPE: [NIGERIA,] swamps, Nupe, without date, *Barter 902* (K; photographs of holotype: UNA!).

Nama macrosepala (A. W. Bennett) Kuntze, Revis. gen. pl. 2:435. 1891.

Herbs, to 8 dm tall, erect, broadly branched. Stems green to brown, often tinged with purple, glabrous. Leaves narrowly lanceolate to lanceolate, 3–8 cm long, 3–12 mm wide, glabrous; apices acuminate to acute; bases obtuse to cordate-clasping. Flowers borne in broadly branching, leafy panicles. Sepals cordate, 5 7.5 mm long, 3–4 mm wide, glabrous. Petals 3.5–4.5 mm long, 2–2.5 mm wide. Ovary glabrous; styles 0.8–1.2 mm long. Capsule cylindrical, usually erect at maturity, 3–4 mm long, 2–3.5 mm broad, glabrous. Seeds broadly cylindrical, 0.4–0.5 mm long, with longitudinal ridges; reticulations uniformly broad and molded into seed surface. Chromosome number unknown.

DISTRIBUTION. Restricted to tropical Africa. Flowering October to December. Figure 10.

DISCUSSION. This is another very distinct species of *Hydrolea,* marked by its cordate-clasping leaf bases and small flowers enveloped by broad, cordate sepals. Like the other African species, *H. macrosepala* is generally glabrous.

ACKNOWLEDGMENTS

I thank Robert R. Haynes and Lincoln Constance for their advice and guidance throughout the course of this research; I also appreciate the helpful comments and suggestions of John D. Bacon and two anonymous reviewers. Special thanks go to Robert R. Haynes, John H. Wiersema, and Charles N. Horn for supplying photographs of type specimens as well as specimens and photographs from Central and South America. Thanks also go to the many curators and their staffs who loaned herbarium specimens or sent photographs of type specimens. These herbaria include: A, APSC, AUA, BM, CHARL, CLEMS, DUKE, F, FARM, FLAS, FSU, GA, GH, GOET, ILL, ILLS, IND, KY, LAF, LL, LSU, MEM, MISS, MO, MUR, MY, NCSC, NCU, NLU, NY, OKL, OKLA, OS, SIU, SMU, TENN, TEX, UARK, UC, UCHT, UMO, US, USF, VDB, VEN, VPI and W.

This paper is adapted from a dissertation submitted to the University of Alabama in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Publication costs were defrayed by a Faculty Development Grant from Samford University.

LITERATURE CITED

Adams, C. D. 1972. Flowering Plants of Jamaica. Univ. of the West Indies, Mona, Jamaica.

Aublet, J. B. C. F. 1775. Histoire des Plantes de la Guiane Francoise. Paris. 4 vols.

Backer, C. A. 1931. Onkruidflora der Javasche Suikerrietgronden, pt. 3. Soerabaja.

———. 1951. Hydrophyllaceae. Fl. Males. Bull. 4: 207–209.

Banerji, M. L., S. Das and G. Sarcar. 1974. Morphological variations in *Hydrolea zeylanica* (Linn.) Vahl and its variety. Geobios (Jodhpur) 1: 179–181.

Bennett, A. W. 1871a. Review of the genus *Hydrolea*, with descriptions of three new species. J. Linn. Soc., Bot. 11: 266–279.

———. 1871b. Hydroleaceae. Pages 392–397, *In*: K. F. P. von Martius, Flora brasiliensis, vol. 7.

Bentham, G. and J. D. Hooker. 1876. Ordo CXI. Hydrophyllaceae. Genera plantarum 2: 825–832.

Brand, A. 1913. Hydrophyllaceae. Pages 1–210, *In*: H. G. A. Engler, Das Pflanzenreich 4, 251. W. Engelmann, Berlin.

———. 1927. *Hydrolea minima* Brand nov. spec. (Hydrophyllaceae). Notizbl. Bot. Gart. Berlin-Dahlem 10: 120.

Britton, N. L. and A. Brown. 1896. An Illustrated Flora of the Northern United States. C. Scribner's Sons, New York. 3 vols.

——— and ———. 1913. An Illustrated Flora of the Northern United States, ed. 2. C. Scribner's Sons, New York. 3 vols.

Brown, R. 1818. Observations, systematical and geographical, on Professor Christian Smith's collection of plants from the vicinity of the river Congo. Pages 420–485, *In*: J. K. Tuckey, Narrative of an Expedition to Explore the River Zaire. London.

Cave, M. S. and L. Constance. 1959. Chromosome numbers in the Hydrophyllaceae. V. Univ. Calif. Publ. Bot. 30: 233–258.

Chester, E. W. 1970. Some new vascular aquatic plants from Tennessee. J. Tennessee Acad. Sci. 45: 6–7.

Chodat, R. and E. Hassler. 1903. Plantae Hasslerianae: Hydrophyllaceae. Bull. Herb. Boissier (ser. 2) 4: 63–64.

Choisy, J. D. 1833. Description des Hydroléacées. Mém. Soc. Phys. Genève 6:95–122.

_____. 1846. Hydroleaceae. Pages 179–185, *In*: A. de Candolle, Ed., Prodromus Systematis Naturalis Regni Vegetabilis, vol. 10. Paris.

Constance, L. 1963. Chromosome number and classification in Hydrophyllaceae. Brittonia 15:273–285.

_____, and T. I. Chuang. 1982. SEM survey of pollen morphology and classification in Hydrophyllaceae (waterleaf family). Amer. J. Bot. 69:40–53.

Correll, D. S. and H. B. Correll. 1972. Aquatic and Wetland Plants of Southwestern United States. Stanford Univ. Press, Stanford, Cal. 2 vols.

_____ and M. C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.

Croat, T. B. 1967. Flora of Panama, part IX: Family 166. Hydrophyllaceae. Ann. Missouri Bot. Gard. 54:415–418.

Datta, N. and M. Manna. 1963. Chromosome determination of plants. Rep. Bot. Surv. India 1963–64:508.

De Jussieu, A. L. 1789. Genera Plantarum. Paris.

Dumortier, B. C. J. 1829. Analyse des Familles des Plantes. J. Casterman, Tournay.

Exell, A. W. 1929. Mr. John Gossweiler's plants from Angola and Portuguese Congo: Hydrophyllaceae. J. Bot. 67: 106.

Fernald, M. L. 1944. Overlooked species transfers and novelties in the flora of eastern North America. Rhodora 46:1–21, 32–57.

_____. 1950. Gray's Manual of Botany, 8th ed. D. van Nostrand Co., New York.

Gibson, D. N. 1967. Flora of Peru: Hydrophyllaceae. Field Mus. Nat. Hist., Bot. Ser. 13 (pt. 5A):101–112.

_____. 1970. Flora of Guatemala: Hydrophyllaceae. Fieldiana, Bot. 24 (pt. 9): 99–111.

Gladstone, P. 1970. Travels of Alexine: Alexine Tinne, 1835–1869. John Murray, London.

Gleason, H. A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. van Nostrand Co., New York.

Godfrey, R. K. and J. W. Wooten. 1981. Aquatic and Wetland Plants of Southeastern United States: Dicotyledons. Univ. of Georgia Press, Athens.

Gray, A. 1875. A conspectus of the North American Hydrophyllaceae. Proc. Amer. Acad. Arts 10: 312–332.

Haines, H. H. 1922. The Botany of Bihar and Orissa, pt. 4. Adlard & Son and West Newman, Ltd., London.

Hasskarl, J. K. 1842. Plantarum genera et species novae aut reformatae javenses. Flora 25: 1–56.

HASSLER, E. 1914. Novitates argentinae. IV. Repert. Spec. Nov. Regni Veg. 13: 237–239.

INAMDAR, J. A. AND R. C. PATEL. 1973. Structure, ontogeny and classification of trichomes in some Polemoniales. Feddes Repert. 83: 473–488.

JAYASURIYA, A. H. M. 1976. New records of some native and naturalized plant species in Sri Lanka. Ceylon J. Sci., Biol. Sci. 12: 15–22.

KAINRADL, E. 1927. Beiträge zur Biologie von *Hydrolea spinosa* L. mit besonderer Berücksichtigung von Fruchtwand und Samememtwicklung. Akad. Wiss. Wien Sitzungsver., Math. – Naturwiss. Kl., Abt. 1, 136: 167–193.

KRISHNAPPA, D. G. 1971. Cytological studies in some aquatic angiosperms. Proc. Indian Acad. Sci. B, 73: 179–185.

KUNTZE, C. E. O. 1891. Revisio Generum Plantarum, vol. 2. Leipzig.

LANJOUW, J. AND F. A. STAFLEU. 1954. Index Herbariorum, pt. 2: Collectors (A–D). I. B. P. T. N., Utrecht.

LEMÉE, A. 1953. Flore de la Guyane Francaise, vol. 3. Paris.

LINNAEUS, C. 1753. Species Plantarum. Stockholm. 2 vols.

_____. 1759. Systema Naturae, ed. 10, vol. 2. Stockholm.

_____. 1762. Species Plantarum, ed. 2, vol. 1. Stockholm.

_____. 1767. Mantissa Plantarum, pt. 1. Stockholm.

LONG, R. W. AND O. LAKELA. 1976. A Flora of Tropical Florida. Banyan Books, Miami.

MACBRIDE, J. F. 1917. Notes on the Hydrophyllaceae and a few other North American spermatophytes. Contr. Gray Herb. 49: 23–59.

MERRILL, E. D. 1918. Species Blancoanae. Bureau of Printing, Manila.

MITRA, J. N. 1945. On the development of the female gametophyte in *Hydrolea zeylanica* Vahl. Curr. Sci. 14: 206.

_____. 1947. A contribution to the life-history of *Hydrolea zeylanica* Vahl. J. Indian Bot. Soc. 26: 51–61.

NASH, D. L. 1979. Hydrophyllaceae. Pages 1–37, *In*: A. Gómez-Pompa, Ed., Flora de Veracruz, fasc. 5.

RADFORD, A. E., H. E. AHLES AND C. R. BELL. 1968. Manual of the Vascular Plants of the Carolinas. Univ. of North Carolina Press, Chapel Hill.

RAFINESQUE, C. S. 1838. Sylva Telluriana. Publ. by the author, Philadelphia.

RAYNAL-ROQUES, A. 1980. Les plantes aquatiques. Pages 63–152, *In*: J. R. Durand and C. Leveque, Flore et Faune Aquatiques de l'Afrique, Sahelo-Soudaniene, vol. 1. O. R. S. T. O. M., Paris.

SARKAR, A. K., N. DATTA AND U. CHATTERJEE. 1973. Chromosome number report. Pages 652–653, *In*: A. Löve, Ed., IOPB Chromosome Number Reports XLII, Taxon 22: 647–654.

SAVAGE, S. 1945. A Catalogue of the Linnaean Herbarium. Taylor & Francis, Ltd., London.

SCHREBER, J. C. D. VON. 1789. Genera Plantarum, vol. 1.

SCHUMACHER, H. C. F. 1827. Beskrivelse af Guineiske Planter. Copenhagen.

SMALL, J. K. 1903. Flora of the Southeastern United States. Publ. by the author, New York.

_____. 1913. Flora of the Southeastern United States, ed. 2. Publ. by the author, New York.

_____. 1933. Flora of the Southeastern United States, ed. 3. Publ. by the author, New York.

SPRENGEL, K. P. J. 1827. Systema Vegetabilium, ed. 16[17], vol. 4. Göttingen.

STAFLEU, F. A. 1967. Taxonomic Literature. I. B. P. T. N., Utrecht.
———, AND R. S. COWAN. 1976. Taxonomic Literature, ed. 2: A–G (vol. 1). Bohn, Scheltema & Holkema, Utrecht.
——— AND ———. 1979. Taxonomic Literature, ed. 2: H-Le (vol. 2). Bohn, Scheltema & Holkema, Utrecht.
——— AND ———. 1981. Taxonomic Literature, ed. 2: Lh-O (vol. 3). Bohn, Scheltema & Holkema, Utrecht.
STANDLEY, P. C. 1928. Flora of the Panama Canal Zone. Contr. U. S. Natl. Herb. 27.
STUCKEY, R. L. 1971. The first public auction of an American herbarium including an account of the fate of the Baldwin, Collins, and Rafinesque herbaria. Taxon 20: 443 459.
SVENSSON, H. G. 1925. Zur Embryologie der Hydrophyllaceen, Borraginaceen und Heliotropiaceen mit besonderer Berücksichtigung auf die Endospermbildung. Uppsala Univ. Arsskr. Mat. Naturv. 2:1–176.
SWARTZ, O. P. 1788. Nova Genera & Species Plantarum seu Prodromus. Stockholm, Uppsala, Abo.
THOUARS [DU PETIT-THOUARS], L.-M. A. A. 1806. Genera Nova Madagascariensia. Paris.
VAHL, M. 1791. Symbolae Botanicae, pt. 2. Copenhagen.
VAN HORN, G. S. 1981. The vascular plant flora of Amnicola Marsh. ASB Bull. 28:84. (Abstract).
VAN STEENIS, C. G. G. J. 1948. Remarks on some generic names used for Malaysian phanerogams. I. Bull. Jard. Bot. Buitenzorg (ser. 3) 17:457 464.
WEATHERBY, C. A. 1942. A list of type specimens in Elliott's herbarium. Contr. Gray Herb. 44:249–262.
WETTSTEIN, R. VON, J. WIESNER AND A. ZAHLBRUCKNER. 1906. Verhandlungen des Internationalen Botanischen Kongresses in Wien 1905. Verlage von Gustav Fischer, Jena.
WILLIAMS, R. O. 1947. Hydrophyllaceae. Flora of Trinidad and Tobago 2: 185-187.

DEPARTMENT OF BIOLOGY
SAMFORD UNIVERSITY
BIRMINGHAM, AL 35229

APPENDIX
DOUBTFUL AND EXCLUDED TAXA

Hydrolea auriculata Sessé & Mociño ex Choisy, Mém. Soc. Phys. Genève 6: 116. 1833 (pro syn. sub *Wigandia kunthii*).
H. caracassana Steudel, Nomencl. 417. 1821 (nom. nud.).
H. congesta Willd. ex Roemer & Schultes, Syst. veg. ed. 16, 6: 192. 1820. = *Nama undulatum* HBK., fide Choisy (1833).
H. crispa Ruiz & Pavon, Fl. peruv. 3:22. 1802. = *Wigandia crispa* (Ruiz & Pavon) HBK., fide Choisy (1833).
H. decurrens Sessé & Mociño ex Choisy, Prodr. 10: 181. 1846 (pro syn. sub *Nama jamaicense*).

H. depauperata Klotzsch ex Schomburgk, Reisen in Britisch-Guiana 3: 1154. 1849 (nom. nud.).
H. dichotoma Ruiz & Pavon, Fl. peruv. 3:22. 1802. = *Nama dichotomum* (Ruiz & Pavon) Choisy, fide Choisy (1833).
H. diffusa Raeuschel, Nomencl. ed. 3, 76. 1797. = ?
H. glabra Smith in Rees, Cycl. 21, pt. 42. 1812 (nom. nud.).
H. hispida Pavon ex Brand, Pflanzenr. 4, 251:135. 1913 (pro syn. sub *Wigandia urens*).
H. jamaicensis Raeuschel, Nomencl. ed. 3, 76. 1797. = *Nama jamaicense* L.
H. latifolia Raf., Atlantic J. 146. 1832 (nom. nud.).
H. leptocaulis Featherman, Bot. surv. La. 100. 1871 (nom. nud.).
H. ludoviciana Featherman, Bot. surv. La. 100. 1871 (nom. nud.).
H. mollis Willd. ex Roemer & Schultes, Syst. veg. ed. 16, 6: 190. 1820 (pro syn. sub *Wigandia caracassana*).
H. montevidensis (Sprengel) Choisy, Prodr. 10:181. 1846. = ?
H. radians Sessé & Mociño ex Choisy, Mém. Soc. Phys. Genève 6:112. 1833 (pro syn. sub *Nama undulatum*).
H. rupincola Sessé & Mociño ex Choisy, Mém. Soc. Phys. Genève 6:112. 1833 (pro syn. sub *Nama undulatum*).
H. scorpioides Sessé & Mociño ex Choisy, Mém. Soc. Phys. Genève 6:117. 1833 (pro syn. sub *Wigandia scorpioides*).
H. spinosa var. *megapotamica* subvar. *speciosa* Brand, Pflanzenr. 4, 251:182. 1913 (nom. nud.).
H. spinosa var. *spinosa* f. *glabrispina* Brand, Pflanzenr. 4, 251:182. 1913 (nom. nud.).
H. spinosa var. *spinosa* f. *latifolia* Raf. ex Brand, Pflanzenr. 4, 251:181. 1913 (nom. nud.).
H. spinosa var. *spinosa* f. *longifolia* Brand, Pflanzenr. 4, 251:182. 1913 (nom. nud.).
H. spinosa var. *spinosa* f. *vulgaris* Brand, Pflanzenr. 4, 251:181. 1913 (nom. nud.).
H. tenella Sessé & Mociño ex Choisy, Prodr. 10:182, 183. 1846 (pro syn. sub *Nama origanifolium*).
H. urens Ruiz & Pavon, Fl. peruv. 3:21. 1802. = *Wigandia urens* (Ruiz & Pavon) HBK., fide Choisy (1833).
H. verticillata Raf., Fl. ludov. 51. 1817. = ?
H. violacea Sessé & Mociño ex Choisy, Mém. Soc. Phys. Genève 6:114. 1833 (pro syn. sub *Nama longiflorum*).
Reichelia montevidensis Sprengel, Syst. veg. ed. 17, 1:940. 1825. = ?
Steris villosa Pavon ex Choisy, Mém. Soc. Phys. Genève 6:108. 1833 (nom. nud.).

RHODORA, Vol. 90, No. 862, 1988

BOOK REVIEW

Case, F. W., Jr. 1987. *Orchids of the Western Great Lakes Region.* 251 pages. Cranbrook Institute of Science, P.O. Box 801, Bloomfield Hills, MI. 48013. ISBN 87737-036-2. ($28.95)

With the publication in 1964 of "Orchids of the Western Great Lakes Region," botanists were presented with a useful guide to species of the region by an author who knew his subject well. The revised edition of 1987 is even better. It is expanded by 100+ pages, supplemented by good quality color photographs of orchids and their habitats and by updated distribution maps; some portions of the text have been extensively rewritten and expanded. There are now several North American regional orchid floras but none cover the range of subjects including ecology and habitat, cultivation and conservation, as thoroughly as does this book.

The 1975 publication of Luer's "The Native Orchids of the United States and Canada" introduced many taxonomic changes which Case has largely followed. The keys, accompanied by line drawings, descriptions and distribution maps, are the working portion of the book which will be found useful by people with a range of backgrounds. Illustrations of habitats are very good and many orchid species are shown in samples of these habitats, giving a sense of place. *Spiranthes* species are often difficult to distinguish; this task is made easier by detailed photographs of inflorescences. Distribution maps are compiled from recent herbarium surveys but many county records are old and some species have not been seen at some of these sites for a half century or longer. It would have been helpful if the dot maps distinguished between older and more recent collections; this differentiation might even whet appetites for rediscovery. Maps are much more useful in this edition now that they have been moved to the appropriate text position rather than being relegated to the end of the text as in the first edition.

For this reviewer the best part of the book is the author's updated discussions of inconstant ecology, including such subjects as the roles of disease, frost, rodents, changing water levels and the depredations of man. There are horror stories of habitat destruction tempered by discussions of the place of some species in temporary and changing environments. Disturbance is relative: it may eliminate

some species and set the stage for colonization by others. The author emphasizes the need for more understanding of orchid ecology as an aid in environmental management. The author's long experience in growing native orchids is well presented in the extensively revised section on cultivation. Some may debate the species he lists as amenable to cultivation, but that is a minor reservation; what grows in Saginaw may languish elsewhere.

This attractive and well written volume is the only current guide to orchids of the western Great Lakes region. It will be of value not only to the orchidophile but to anyone wishing to know more about habitat diversity of the region.

WARREN STOUTAMIRE
BIOLOGY DEPARTMENT
UNIVERSITY OF AKRON
AKRON, OHIO 44325

RHODORA, Vol. 90, No. 862, 1988

BOOK REVIEW

Duncan, Wilbur H. and Marion B. Duncan. 1987. *Seaside Plants of the Gulf and Atlantic Coasts*. 409 pp. Smithsonian Institution Press, Washington, DC. (Price: $45.00, cloth; 29.95, paper)

This volume covers the vascular seaside plants found along the Gulf and Atlantic coasts from the Texas-Louisiana border to Plum Island, Massachusetts with the exception of peninsular Florida. The definition of "seaside" used to define the plants covered is "that area abutting the sea or strongly influenced by it."

The format of the book is good and of use to both professional botanists and amateurs. There are a series of keys designed to identify the family, genus, or species. In many cases, once the family or genus has been identified, one must refer to the short treatment of the taxon in the body of the book. Descriptions for the common taxa encountered are included, occasionally accompanied by a line drawing.

This publication is well illustrated with excellent color photographs of the major taxa identified. These are top quality photographs which make this volume particularly valuable to the amateur. For the professional botanist this is more than a picture book since it includes keys and descriptions. If more is desired for identification or description, one can easily refer to more comprehensive floras at this point.

An interesting introduction which includes comments dealing with various aspects of the coastal plain, plant adaptations and coastal topography, precedes the keys. There is also a glossary and a series of illustrations depicting various vegetative structures. I recommend this book to all those interested in the coastal flora.

C. BARRE HELLQUIST
DEPARTMENT OF BIOLOGY
NORTH ADAMS STATE COLLEGE
NORTH ADAMS, MASSACHUSETTS 01247

Vol 90, No. 861, including pages 1–112, was issued January 29, 1988

The New England Botanical Club
22 Divinity Avenue
Cambridge, Mass. 02138

The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 90th year and contains about 500 pages a volume.

Membership is open to all persons interested in systematics and field botany. Annual dues are $25.00, including a subscription to RHODORA. Students may apply for a Student Membership at $10.00 a year, which does not include a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

Regular Member	$25.00
Family Membership	$35.00
Student Member	$10.00
For this calendar year	_____
For the next calendar year	_____

Name _____

Address _____

City & State _____ Zip _____

Special interests (optional):

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8″) **throughout** including tables, figure legends, and literature citations. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

RHODORA April 1988 VOL. 90, No. 862

CONTENTS

A survey of floral variation in five populations of Podostemum ceratophyllum Michx. (Podostemaceae)
C. Thomas Philbrick and *A. Linn Bogle* 113
Typification of J. Lunell's names in Adicea (Urticaceae)
David E. Boufford 123
New chromosome counts in Acer (Maple) species, sections Acer and Goniocarpa
Frank S. Santamour, Jr. 127
The genus Antennaria (Asteraceae: Inuleae) in western North America. II. Additional chromosome counts
J. G. Chmielewski and *C. C. Chinnappa* 133
Spiranthes nebulorum (Orchidaceae), a new species from southern Mexico and Guatemala
Paul M. Catling and *Vivian R. Catling* 139
A first report for Carex hypsipedos (Cyperaceae) in Argentina and Bolivia and the status of C. phalaroides var. parvula in southern South America
Gerald A. Wheeler 149
The corect name for Elliott's Goldenrod
Leonard J. Uttal and *Duncan M. Porter* 157
A monograph of Hydrolea (Hydrophyllaceae)
L. J. Davenport 169
BOOK REVIEWS
Orchids of the western Great Lakes region
Warren Stoutamire 209
Seaside plants of the Gulf and Atlantic coasts
C. Barre Hellquist 211
NEBC Membership Application Form 213
Instructions to Contributors . . . . . inside back cover

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 90 July 1988 No. 863

The New England Botanical Club, Inc.

22 Divinity Avenue, Cambridge, Massachusetts 02138

RHODORA

NORTON H. NICKERSON, Editor-in-Chief

Associate Editors

DAVID S. BARRINGTON
A. LINN BOGLE
DAVID E. BOUFFORD
WILLIAM D. COUNTRYMAN
GARRETT E. CROW
RICHARD A. FRALICK
GERALD J. GASTONY
C. BARRE HELLQUIST
MICHAEL W. LEFOR
ROBERT T. WILCE

ISSN 0035-4902

RHODORA.—Published four times a year, in January, April, July, and October by the New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138. Second Class postage paid at Boston, MA. A journal of botany devoted primarily to the flora of North America. Price $25.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to 22 Divinity Avenue, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related areas, and articles concerned with systematic botany and cytotaxonomy in their broader implications will be considered. Brevity is urged; please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Fifty reprints of each article are supplied free of charge. Authors may arrange with Lexington Press for additional copies. RHODORA assesses page charges.

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

POSTMASTER: Send address changes to RHODORA, 22 Divinity Avenue, Cambridge, MA 02138.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS 02173

Cover Illustration

Eupatorium leucolepis var. *novaeangliae* is an endemic New England taxon restricted to upper margins of sandy-peaty coastal plain ponds. Currently vouchered from 7 ponds in MA and 5 in RI (several historical stations are extirpated), New England Boneset is a candidate for federal listing. The nominate variety occurs from Long Island in NY (very rare) and southern NJ to FL and LA.

Original artwork by Caren Caljouw

Rhodora

(ISSN 0035-4902)

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 90 July 1988 No. 863

A NEW *PILEA* (URTICACEAE) FROM HISPANIOLA

JAMES D. SKEAN, JR.[1] AND WALTER S. JUDD

ABSTRACT

Pilea howardiana is described and illustrated from Parc National Pic Macaya in the Massif de la Hotte of Haiti. The species is compared to its presumed closest relative, *P. formonensis,* from which it differs primarily in its smaller size and herbaceous (vs. suffrutescent) habit, gray-green (vs. tan) older stems, shoots that are more densely pubescent, leaves with flat to slightly adaxially impressed (vs. strongly impressed) veins, and stipules lacking a prolonged chartaceous apex. Both species are known only from the Morne Formon region, an area of exceptional endemism.

Key Words: *Pilea,* Urticaceae, flora of Hispaniola (Haiti)

INTRODUCTION

The genus *Pilea* Lindley is the largest in the Urticaceae, *sensu stricto,* comprising some 400 species of herbs or subshrubs native primarily to tropical regions (Engler, 1888). Members of the genus lack stinging hairs and have carpellate flowers with inflexed staminodia, which, as a result of changes in turgor pressure, may straighten quickly and forcibly eject the achene in a manner similar to the way stamens discharge pollen explosively from the staminate flowers (Miller, 1971; Mosebach, 1932). Species of *Pilea* are most commonly found growing in shallow substrates on rock in moist montane areas. The genus is of relatively little economic importance, but several species, such as *P. cadierei* Gagnepain & Guillaumin (aluminum-plant) and *P. microphylla* (L.) Liebm. (artillery-plant), are popular ornamentals. The latter is a common greenhouse weed.

[1]Present address: Department of Biology, Albion College, Albion, MI 49224

Although pileas are conspicuous elements of many plant communities throughout the tropics, they have received little taxonomic attention (Miller, 1971). The only monographs of the genus are those of Weddell (1856, 1869), who recognized 139 and 156 species, respectively. This lack of recent monographic study is evidenced by modern estimates of the size of *Pilea,* which vary from 200 (e.g., Cronquist, 1981) to 400 (e.g., Willis, 1973), though the circumscription of the genus has remained relatively stable. Without giving an approximation of the number of species, Miller (1971) stated that over 600 had been described, but estimated that the actual number was much lower. Ellsworth P. Killip, perhaps the premier student of *Pilea* in this century, described many new taxa from Central and South America (Killip, 1925, 1936, 1939, 1960) and recognized 112 species from the Andes (Killip, 1939), a center of diversity for the genus.

The West Indies, especially the Greater Antilles, are also a major center of diversity for *Pilea* (Morton, 1945). Nearly a quarter of the genus (100 spp., 83 endemic) is said to occur on Hispaniola (Moscoso, 1943). Following Hispaniola in species number are Cuba (65 spp., 52 endemic; León and Alain, 1951), Jamaica (48 spp., 37 endemic; Adams, 1972), and Puerto Rico (16 spp., 4 endemic; Liogier and Martorell, 1982).

Our recent field work on Hispaniola in Parc National Pic Macaya in the Massif de la Hotte of Haiti (Judd, 1987), not surprisingly, has resulted in the discovery of an apparently undescribed species of *Pilea,* which is described and illustrated below.

Pilea howardiana Skean & Judd, *sp. nov.* (Figure 1)

Species haec a Pilea formonensi Urban & E. Ekman differt habitu herbaceo, caulibus griseo-viridibus, surculis densius pubescentibus, stipulis uniformius viridibus, et venis foliorum supra planis vel leviter impressis.

Erect, fleshy or weakly suffrutescent ± monoecious herb to ca. 30 cm high. *Indumentum* of silvery, unbranched, unicellular hairs, to ca. 2.2 mm long, which dry flattened and ribbon-like, and scattered, golden-brown, globular, sessile, multicellular glands, to ca. 0.6 mm across. *Stems* ± terete or slightly flattened, gray-green, portions bearing leaves ca. 2 mm in diam, with 2 longitudinal grooves ca. 0.3

mm wide, on opposite faces of internode positioned 90° from attachment of leaves of adjacent upper node, with conspicuous fusiform or ± cylindrical, straight to strongly curved cystoliths, 0.04–0.24 mm long, ca. 0.04 mm wide, the surface pubescent; internodes (0.5)1–3(4.3) cm long. *Leaves* opposite, stipulate; blade (1.2)1.7–4.4(5.1) cm long, (0.9)1.5–3(3.5) cm wide, ovate, fleshy, the apex acute or obtuse, the base obscurely cordate or rounded, rarely obtuse, the margin ± entire, moderately to densely pubescent (with 5–10 hairs/mm at widest point of leaf); venation acrodromous, basal, with the midvein, 2 secondary veins, and percurrent tertiary veins not or only slightly impressed adaxially, with midvein, secondary veins, and tertiary veins raised abaxially; adaxial surface essentially glabrous except occasionally for a few scattered hairs near the pubescent margin and inconspicuous, scattered, minute glands located primarily on veins, the cystoliths conspicuous; abaxial surface moderately to densely pubescent with hairs concentrated on veins, and with scattered, minute glands; petiole (2)6–28(44) mm long, canaliculate, pubescent; stipules ovate, 2.3–3.3 mm long, 0.8–2 mm wide, the central green thickened portion occupying over 3/4 of total stipule length, the apex obtuse, often slightly toothed. *Inflorescences* axillary, predominately unisexual, many-flowered, bracteate clusters of cymes with indumentum like stems, but generally not as densely covered with hairs, the bracts ovate, green to hyaline, 0.6–1.7 mm long, 0.4–1.1 mm wide, the apices obtuse with several small teeth or acuminate, lacking elongate hairs, but often conspicuously glandular. *Staminate inflorescences* usually composed of 1–3 globose heads, each ca. 4–6 mm in diam, the peduncle 1.8–3 cm long. *Staminate flower* ca. 0.9 mm across at anthesis, sessile or borne on a pedicel to ca. 1 mm long; tepals 4, greenish or tinged with red, ± isomorphic, narrowly triangular, with acute apices, fused basally, the fused portions saccate, clasping the inflexed stamens in bud, the free portions 0.5–0.6 mm long, ca. 0.45 mm wide; stamens 4, opposite tepals, white, folded adaxially in bud, the filaments 0.4–0.5 mm long, ca. 0.08 mm wide, narrowly triangular, flattened, the anthers 0.3–0.4 mm long, 0.25–0.35 mm wide, basifixed, but appearing versatile due to deeply sagittate bases, dehiscing by means of 2 longitudinal slits. *Carpellate inflorescences* paniculate, ± secund, less densely aggregated, 1.5–3.5 cm long, 0.3–1.4 cm wide, the peduncle

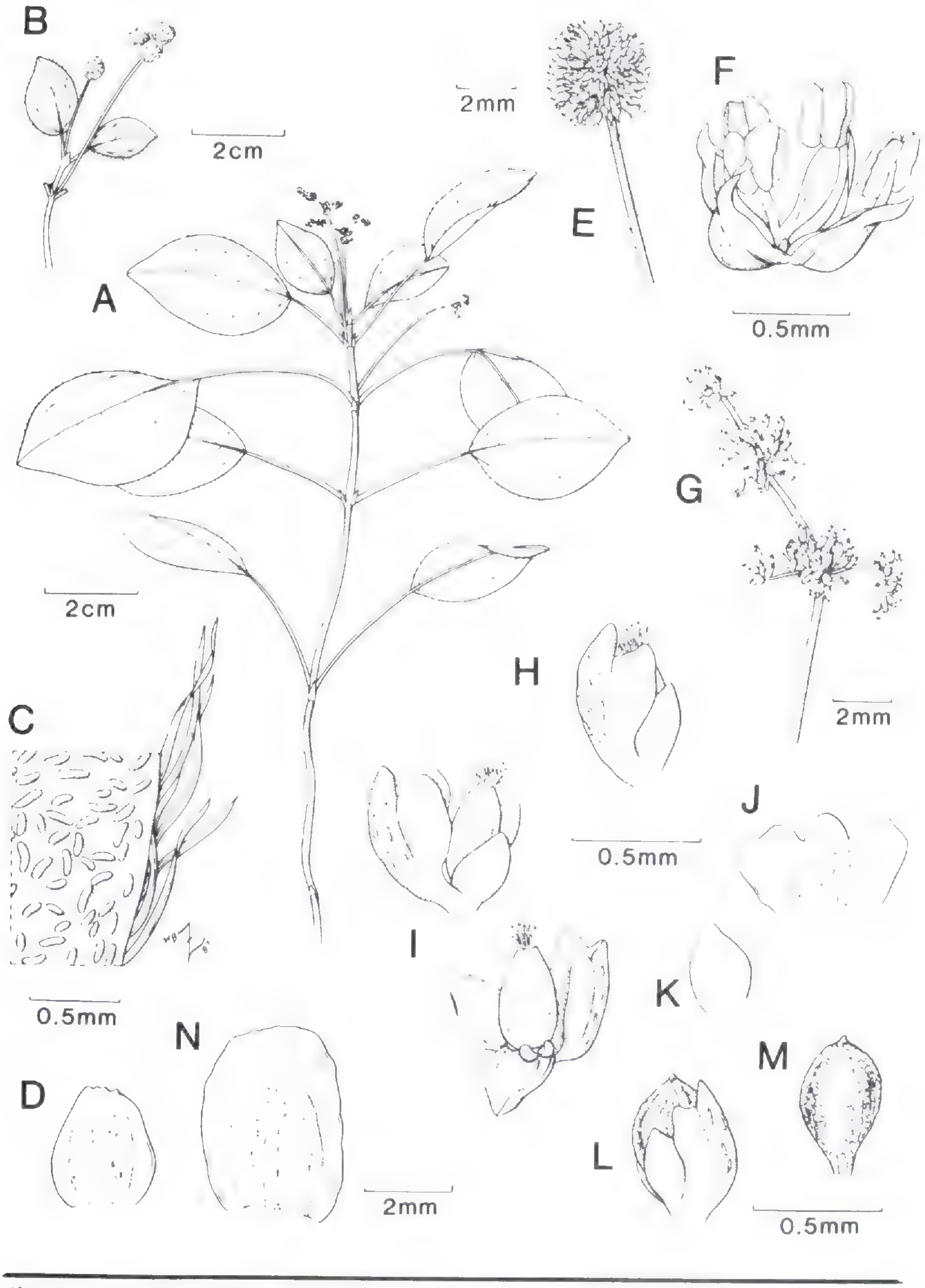
1.2–2.4 cm long, often with an occasional staminate flower intermixed; *Carpellate flowers* ± sessile; tepals 3, dimorphic, obovate, fused basally, with acute apices, the largest tepal saccate, 3-lobed, the free portion when flattened ca. 0.4 × 0.65 mm, the middle lobe greenish, ca. 0.2 mm wide, the lateral lobes hyaline, ca. 0.22 mm wide, the 2 smaller tepals hyaline, with free portions ca. 0.35 × 0.25 mm; staminodia 3, folded adaxially before fruit dispersal, appearing as small rounded projections ca. 0.07 mm high at ovary base; ovary appearing unicarpellate, clasped by bases of tepals; stigma penicillate, often tinged with red, the elongated papillae ca. 0.1 mm long, soon caducous. *Achenes* slightly obovoid, lenticular, ca. 0.6 × 0.5 mm, brown, slightly roughened-reticulate.

TYPE: HAITI. Département du Sud: Massif de la Hotte, Parc National Pic Macaya, Bwa Formon (= Bois Formond), i.e., woods near settlement of Formon on plain S of Morne Formon, wet forest on dog-toothed limestone, ca. 1000 m elev., 1 Jun 1984 (fl, fr), *Skean 1199* (HOLOTYPE: FLAS; ISOTYPES: GH, NY, S).

ADDITIONAL SPECIMENS EXAMINED: **Haiti.** Département du Sud: Massif de la Hotte, Parc National Pic Macaya, Bwa Formon, 950 1040 m elev., *Judd 3531* (FLAS, JBSD); *ibid.*, N slope of Morne Formon in ravine of Rivière du Sud, disturbed broad-leaved cloud forest, ca. 1500 m elev., *Skean 1348* (EHH, FLAS, JBSD).

ETYMOLOGY: The specific epithet honors Dr. Richard Alden Howard (b. 1917), noted botanist of the Arnold Arboretum, Harvard University, and student of the West Indian flora. Dr. Howard and his wife Betty provided logistical support and gracious hospitality to the second author during the second author's visit to the Harvard University Herbaria (A, GH) for the purpose of identifying our collections from Haiti.

Figure 1. **A–M.** *Pilea howardiana*. **A.** Habit, carpellate plant. **B.** Fertile portion of staminate plant. **C.** Detail of leaf adaxial surface showing cystoliths and marginal hairs. **D.** Stipule – note thickened central portion occupying nearly entire length of stipule. **E.** Staminate inflorescence. **F.** Staminate flower. **G.** Carpellate inflorescence. **H.** Carpellate flower. **I.** Carpellate flower with tepals teased apart, two views — note larger enveloping 3-lobed tepal, smaller lateral tepals and reduced, folded stamino-



dia. **J.** Enveloping 3-lobed tepal of carpellate flower, expanded, abaxial view. **K.** Lateral tepal of carpellate flower, abaxial view. **L.** Achene surrounded by tepals. **M.** Achene, slightly immature.

N. *P. formonensis* stipule, abaxial view — note thickened central portion extending only ca. 2/3 of stipule length. (Drawings for A, C, D, G, H, I, J, K, L, M from holotype; for B, E, F, from *Skean 1348;* for N, from *Judd 1448*).

Pilea howardiana is known only from Bwa Formon and Morne Formon in the Parc National Pic Macaya of the Massif de la Hotte, Haiti, where it is an occasional to locally common herb in *rak bwa,* i.e., moist hardwood forests on karst domes, slopes, or in ravines in areas of dog-toothed limestone (at ca. 1000 m elev.), and in disturbed broad-leaved cloud forests (over limestone) at higher elevations (to ca. 1500 m). The *rak bwa* vegetation is floristically similar to the "wet forest on limestone" described by Howard (1973). For detailed discussions of these vegetation types, along with lists of characteristic species, important endemics, and recently described taxa, see Judd (1986a, 1986b, 1987), Judd and Skean (1987a, 1987b) and Skean and Judd (1986, 1988). It is hoped that the recent establishment of Parc National Pic Macaya will allow the preservation of at least a portion of the diverse and highly endemic flora of the La Hotte region.

Pilea howardiana is very similar to *P. formonensis*, another endemic species of the Morne Formon region, and the two are likely closely related. *Pilea howardiana* is readily distinguished by (1) its herbaceous (vs. suffrutescent) habit, (2) gray-green (vs. tan) mature stems, (3) stems and leaves that are more densely pubescent, e.g., 5–10 hairs/mm along leaf margin measured at widest point of leaf, thus densely overlapping (vs. 1 3 hairs/mm and non-overlapping), (4) leaves with flat to slightly adaxially impressed (vs. strongly impressed) veins, and (5) stipules lacking a prolonged chartaceous apex, i.e., with the central, green, thickened portion occupying over 3/4 of the total stipule length, (Figure 1D) (vs. stipules with a prolonged chartaceous apex, i.e., with the central, green, thickened portion occupying only ca. 2/3 of total stipule length, (Figure 1N). The two species appear to be isolated elevationally since *P. formonensis* occurs in a mosaic of high elevation cloud forests-moist pine forests from ca. 1700 2200 m, while *P. howardiana* occurs in *rak bwa* and disturbed cloud forests-thickets at 950 1500 m elevation.

The discovery of *Pilea howardiana* brings the number of species of *Pilea* known from Parc National Pic Macaya to twelve; these are: *P. baltenweckii* Urban, *P. distantifolia* Urban, *P. domingensis* Urban, *P. formonensis, P. hepatica* Urban & E. Ekman, *P. howardiana, P. leptocardia* Urban, *P. microphylla* (L.) Leibm. (including several diverse morphological entities), *P. parietaria* (L.) Blume, *P. serpyllacea* (HBK.) Leibm., *P. stolonifera* (Sw.) Wedd., and *P.* cf. *torbeciana* Urban & E. Ekman (Judd, 1987).

ACKNOWLEDGMENTS

We thank Charles A. Woods of the Florida State Museum, coordinator and principal investigator of the U.S.A.I.D.–sponsored project, *Biogeophysical Inventory of the National Parks of Haiti,* who organized the field trips on which this species was collected. Dan and Tia Cordier, and Paul Paryski all provided valuable assistance in the Morne Formon region. We thank Norris H. Williams and Kent D. Perkins for making available the herbarium facilities of the University of Florida (FLAS), the curator of the herbarium of the Swedish Museum of Natural History (S) for a loan of comparative material, and Michael Canoso, Richard A. Howard, Walter Kittredge, and Carroll E. Wood for their assistance during the visit of the second author to the Harvard University Herbaria (A, GH). We also thank Norton G. Miller and two anonymous reviewers for their helpful comments on the manuscript. Finally we thank Wendy B. Zomlefer for her excellent illustration and helpful comments.

LITERATURE CITED

Adams, C. D. 1972. Flowering Plants of Jamaica. Univ. West Indies, Mona.

Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

Engler, A. 1888. Urticaceae. Nat. Pflanzenfam. III. 1: 98–118.

Howard, R. A. 1973. The vegetation of the Antilles. Pp. 1–38. *In:* A. Graham, Ed., Vegetation and Vegetational History of Northern Latin America. Elsevier Scientific Publishing Co., Amsterdam.

Judd, W. S. 1986a. A new species of *Wallenia* (Myrsinaceae) from Haiti. Sida 11: 329–333.

_____. 1986b. First report of *Micropholis polita* (Sapotaceae) and *Hamelia ventricosa* (Rubiaceae) from Hispaniola. Moscosoa 4: 222–225.

_____. 1987. Floristic Study of Morne la Visite and Pic Macaya National Parks, Haiti. Bull. Florida State Mus., Biol. Sci. 32: 1–136.

_____, and J. D. Skean, Jr. 1987a. Two new species of *Meriania* (Melastomataceae) from Hispaniola. Syst. Bot. 12: 374–380.

_____ and _____. 1987b. Three new angiosperms from Parc National Pic Macaya, Massif de la Hotte, Haiti. Bull. Florida State Mus., Biol. Sci. 32: 137–150.

Killip, E. P. 1925. New tropical American species of Urticaceae. J. Wash. Acad. Sci. 15: 289–299.

_____. 1936. New species of *Pilea* from the Andes. Contr. U. S. Nat. Herb. 26: 367–394.

_____. 1939. The Andean species of *Pilea.* Contr. U. S. Nat. Herb. 26: 475–530.

_____. 1960. Urticaceae. *In:* R. E. Woodson and R. W. Schery, Eds., Flora of Panama. Ann. Missouri Bot. Gard. 47: 179–198.

León, Hno. and Hno. Alain. 1951. Flora de Cuba. Vol. 2. Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 11: 1–456.

Liogier, A. H. and L. F. Martorell. 1982. Flora of Puerto Rico and Adjacent Islands: A Systematic Synopsis. Univ. de Puerto Rico, Rio Piedras.

Miller, N. G. 1971. The genera of Urticaceae in the southeastern United States. J. Arnold Arbor. 52: 40 68.

Morton, C. V. 1945. New species of *Pilea* from Cuba. Revista Soc. Cub. Bot. 2: 2–10.

Mosebach, G. 1932. Über die Schleuderbewegung der Explodierenden Staubgefässe und Staminodien bei einigen Urticaceen. Planta 16: 70–115.

Moscoso, R. M. 1943. Catalogus Florae Domingensis. Parte I. Spermatophyta. L. and S. Printing, New York.

Skean, J. D., Jr. and W. S. Judd. 1986. A new *Mecranium* (Melastomataceae) from Hispaniola. Brittonia 38: 230–237.

_____ and _____. 1988. A new Salvia (Labiatae) from Hispaniola. Brittonia 40: 16–21.

Weddell, H. A. 1856. Monographie de la famille des Urticées. Arch. Mus. Hist. Nat. Paris 9: 1 400.

_____. 1869. Urticaceae. *In:* A. P. de Candolle, Ed., Prodromous 16: 32–235.

Willis, J. C. 1973. A Dictionary of the Flowering Plants and Ferns, 8th edition. Revised by H. K. Airy-Shaw. Cambridge Univ. Press, Cambridge.

DEPARTMENT OF BOTANY
220 BARTRAM HALL EAST
UNIVERSITY OF FLORIDA
GAINESVILLE, FL 32611

RHODORA, Vol. 90, No. 863, 1988

DESCRIPTION AND DISTRIBUTION OF *EUPHRASIA STRICTA* IN NORTH AMERICA

STEPHEN R. DOWNIE[1] AND JOHN MCNEILL

ABSTRACT

The origin, subsequent migratory history and present-day distribution of *Euphrasia stricta* J. P. Wolff ex J. F. Lehm. is presented along with its taxonomic description. Introduced into eastern Maine during the 18th or 19th centuries, its range has expanded westward to southcentral Ontario and northward to the Gaspé Peninsula of Québec. In North America, the species is readily characterized by its erect, cuneate, narrowly ovate to ovate-lanceolate glabrous leaves and bracts possessing long aristate teeth.

Key Words: Scrophulariaceae, *Euphrasia stricta*, taxonomy, distribution, North America

In the course of preparing a manuscript on the status of *Euphrasia borealis* (Towns.) Wettst. and *E. nemorosa* (Pers.) Wallr. in relation to *E. stricta* J. P. Wolff ex J. F. Lehm. (Downie et al., 1987), it came to our attention that the precise circumscription of *E. stricta* is not well understood in North America. This misunderstanding was reflected in the many erroneously identified herbarium specimens we saw. Consequently, statements of its range in North America are inaccurate. Moreover, all herbarium collections examimed from Ontario and most from Québec are of recent date, suggesting that these plants have recently migrated into these regions. The purpose of this paper is to provide a precise delineation of this taxon, and by mapping herbarium records and field collections at approximately 20 to 30 year intervals, to ascertain its origin, subsequent migratory history, and present-day distribution.

Many floras (e.g. Fernald, 1950; Gleason, 1952; Gleason and Cronquist, 1953; Marie-Victorin, 1964) have recognized *Euphrasia americana* Wettst. and *E. canadensis* Towns. as ubiquitous throughout the northeastern United States and adjacent Canada. In their revision of the North American species of *Euphrasia*, Sell and Yeo (1970) discovered that the plants to which these names were applied were similar to those found in Europe, and consequently rejected the names *E. americana* and *E. canadensis* in favour of the Euro-

[1]Present address: Dept. of Biology, Univ. of Michigan, Ann Arbor, MI 48109.

pean *E. nemorosa* and *E. borealis*. Recent evidence using multivariate techniques does not support the recognition of *E. nemorosa* and *E. borealis* as separate taxa (Downie et al., 1987). These plants should be treated as a single species, for which the correct name is *E. nemorosa*. *Euphrasia stricta* is, however, morphologically distinct from *E. nemorosa*.

The following names that have been used in North America are all synonyms of *Euphrasia stricta* J. P. Wolff ex J. F. Lehm.: *E. stricta* Host; *E. rigidula* Jord.; *E. condensata* Jord.; and, in part, *E. officinalis* L. *sensu* Gleason and Cronquist (1953). Although no type material of *E. stricta* has been traced (Sell and Yeo, 1970). application of the name can be determined with fair certainty from the original description.

In most of northwestern Europe, *Euphrasia stricta* is a variable species and many local and regional races (Karlsson, 1976; 1986; Yeo, 1978), and infraspecific taxa (Karlsson, 1984) have been described. In North America, however, it is generally unvarying and readily recognized by its erect, narrowly ovate to ovate-lanceolate glabrous leaves, and bracts with long-aristate teeth. The North American plants appear to resemble *E. stricta* var. *stricta* of European authors.

DESCRIPTION OF *EUPHRASIA STRICTA*

STEM rigid and erect, up to 3 dm, usually dark purple with (0–) 1–5 pairs of erect branches from the middle and upper nodes. CAULINE INTERNODES (1–) 5–27 (–34) mm long, usually 1 3 times as long as the subtending leaves, rarely shorter, flowering beginning at node 4–12 (15). FLORAL INTERNODES (2–) 5–18 mm long, 1–2 times as long as the subtending bracts. CAULINE LEAVES 4–10 mm long, 2–8 mm wide, erect, glabrous, narrowly ovate to ovate-lanceolate, cuneate, the margins serrate with 3–5 pairs of antrorse aristate teeth, (0.3–) 1–2 (–2.5) mm long, with an obtuse or acute terminal lobe. BRACTS 4.5 9.5 mm long, 3 6.5 mm wide, erect, glabrous, often appressed to the calyx and usually purple above, narrowly ovate to trullate, cuneate, the margins serrate with 4–5 pairs of antrorse, long-aristate teeth, 0.8–2.5 mm long, with an acute or acuminate terminal lobe. CALYX (4) 5 7 mm long, glabrous or minutely scabrid with long, fine aristate teeth, the teeth (2–) 2.5 3.5 (–4) mm long, the veins sometimes flushed with purple and margins often black. COROLLA (4) 6.5–9 mm long, exceeding the bracts, the tube

3–5 mm long; upper lip white and usually much suffused with lilac; lower lip 3–7 mm wide, white with deep-violet lines, and with wide-spreading lateral lobes, the lobes 1–2.5 mm deep. CAPSULE (2.5–) 4–6.5 mm long, (1–) 1.5–2.5 (–3) mm wide, glabrous, narrowly oblong, retuse to truncate, shorter than the calyx. SEEDS (11–) 16–30 per capsule, 1–1.6 mm long.

PAST MIGRATORY HISTORY AND PRESENT-DAY DISTRIBUTION

The following list of collection localities was compiled from our field work in Atlantic Canada and Maine, and from specimens we have seen and determined from the following herbaria: ACAD, CAN, DAO, GH, MT, MTMG, NEBC, NHA, OTT, and SFS. Mapping these localities according to date of collection (Figures 1, 2) gives some indication of the migratory history of *Euphrasia stricta* over this century.

1901–1930

Maine

Cumberland Co., Brunswick 26 Aug. 1913 *K. Furbish s.n.* (NEBC). Hancock Co., Swans Island 12 Aug. 1918 *A. H. Norton 12440* (NHA); Swans Island Aug. 1910 *K. Furbish s.n.* (NEBC). Kennebec Co., Clinton 15 Aug. 1907 *R. C. Bean 2745* (NHA). Knox Co., Matinicus Island 16 Aug. 1916 *E. B. Chamberlain & A. H. Norton 11610* (NHA). Waldo Co., Islesboro 14 Aug. 1913 *M. L. Fernald 8195* (NHA). Johns Island 15 Aug. 1918 *A. H. Norton s.n.* (NHA).

New York

St. Lawrence Co., Waddington 24 July 1916 *O. P. Phelps 1624* (CAN).

1931–1950

Maine

Hancock Co., Stonington, Deer Island 10 Sept. 1935 *A. R. & M. S. Hodgdon 2412* (NEBC, NHA). Washington Co., Lambert Lake 8 Aug. 1940 *C. H. Knowlton s.n.* (MT).

Pennsylvania

Pike Co., N. Notch Village, 7 mi. N. W. Porters Lake 20 Aug. 1940 *E. T. Wherry s.n.* (GH).

Québec

Châteauguay Co., Saint Chrysostome 30 Aug. 1942 *Fr. Marie-Victorin, Fr. Rolland-Germain & M. Raymond 56035* (CAN, MT); Saint Chrysostome 14 Sept. 1933

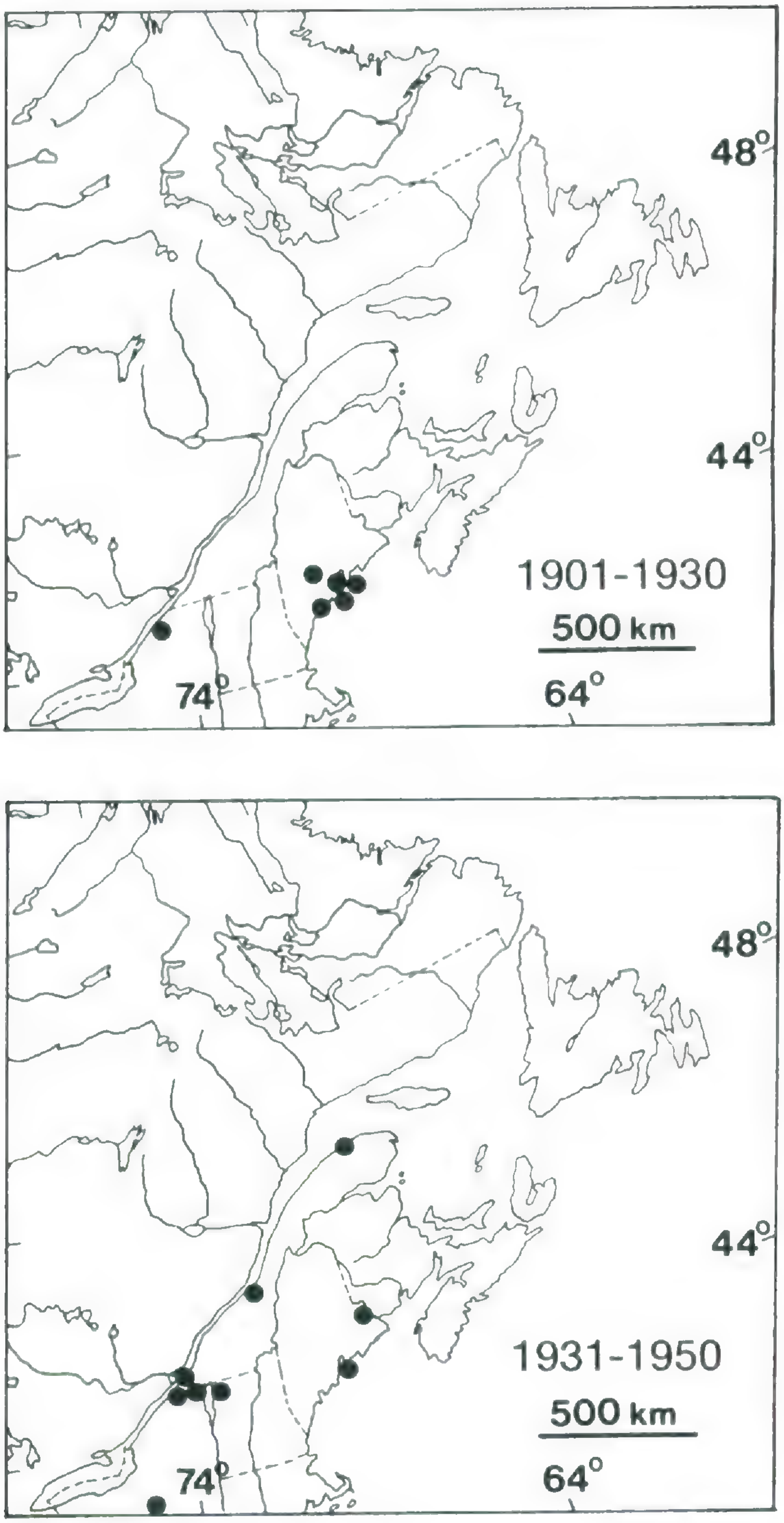
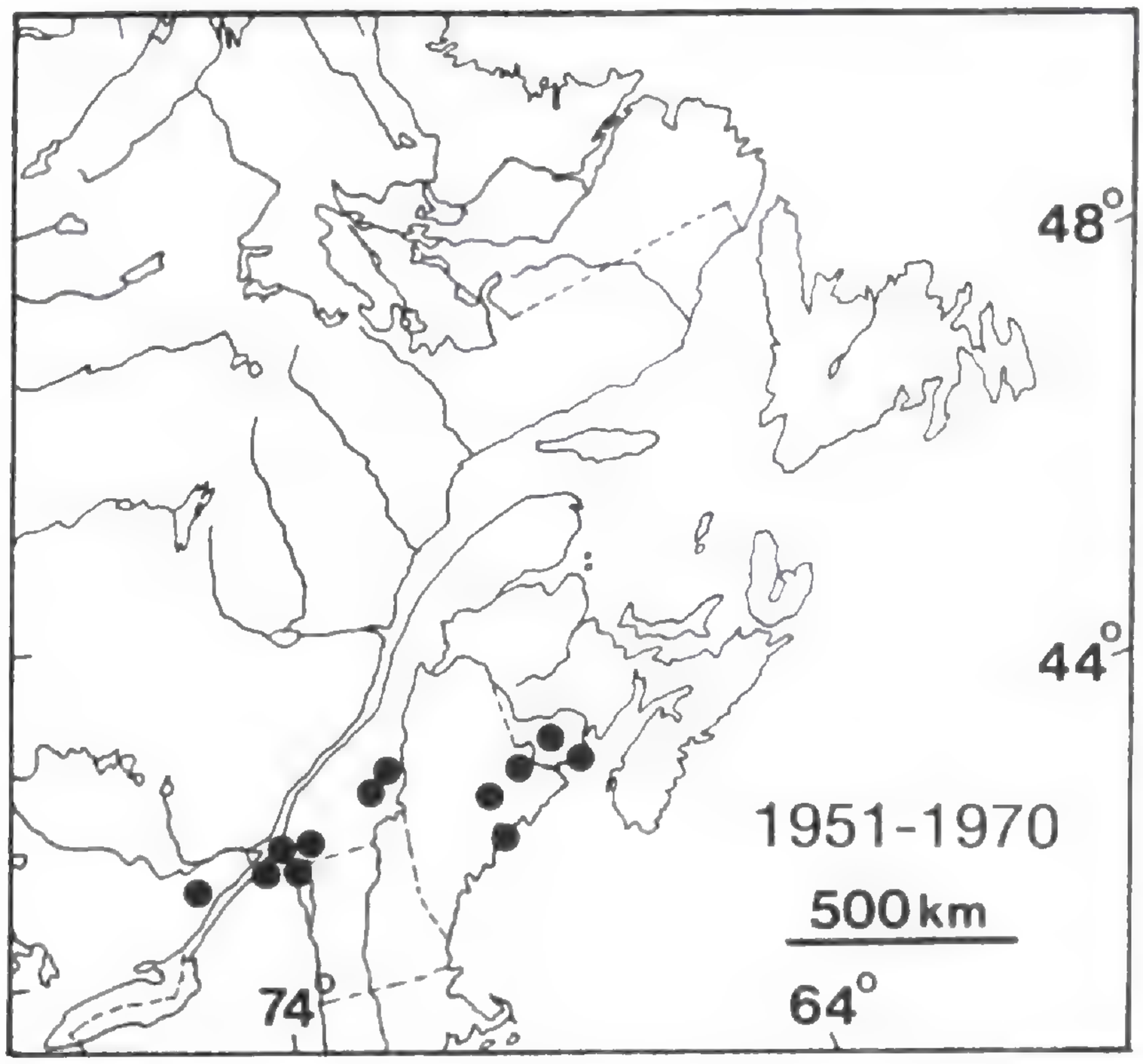


Figure 1. Collection localities of *Euphrasia stricta:* A. from 1901 to 1930; B. from 1931 to 1950. Each dot may represent more than one locality.



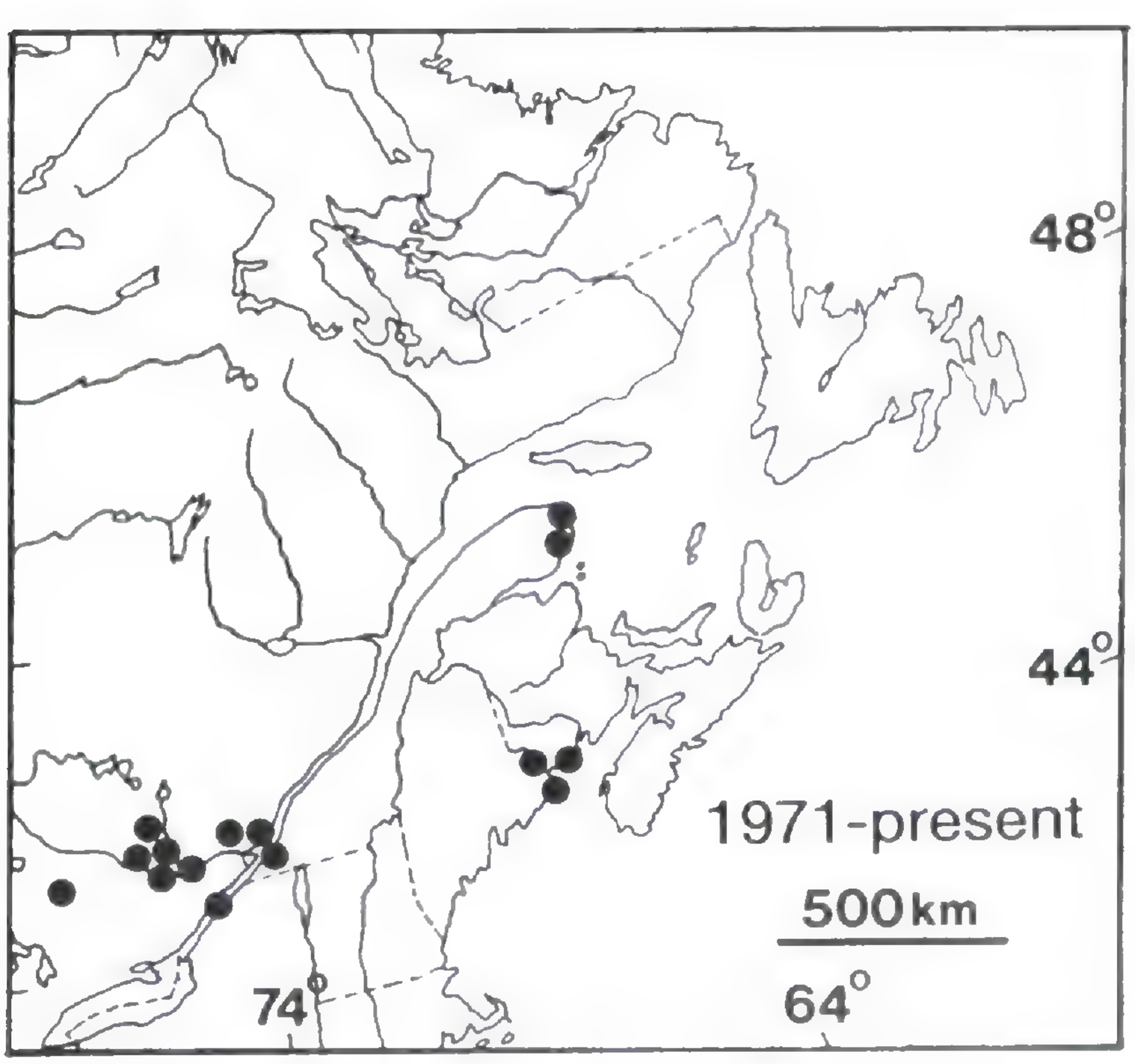


Figure 2. Collection localities of *Euphrasia stricta:* A. from 1951 to 1970; B. from 1971 to present. Manitoulin District not shown. Each dot may represent more than one locality.

Fr. Bernard-Louis s.n. (GH, MT); Saint Chrysostome 14 Sept. 1933 *E. Rouleau 811* (DAO, GH, MT); Saint Chrysostome 14 Sept. 1933 *M. Racine s.n.* (MT); Saint Chrysostome 7 Sept. 1942 *Fr. Marie-Victorin, Fr. Rolland-Germain & M. Raymond 56015* (MT). Gaspé-Ouest Co., Cap-Chat 5 Aug. 1953 *Fr. Samuel 3019* (MT). Huntingdon Co., Covey Hill 10 Sept. 1949 *L. M. Terrill 6082* (DAO). Laprairie Co., Laprairie 11 Sept. 1940 *Fr. Marie-Victorin, Fr. Rolland-Germain & B. Boivin 4232* (GH, MT). Lévis Co., Saint Jean Chrysostome 14 Sept. 1933 *Fr. Bernard-Louis 224* (SFS). Missisquoi Co., Missisquoi (Bay) 5 Sept. 1942 *Fr. Marie-Victorin, Fr. Rolland-Germain & M. Raymond 56192* (GH, MT).

Vermont

Grand Isle Co., E. Alburg 14 Sept. 1935 *A. S. Pease 25348* (NEBC).

1951–1970

Maine

Penobscot Co., Bradley 23 Sept. 1959 *A. E. Brower s.n.* (NEBC). Waldo Co., Islesboro, Keller (Hermit) Point 13 Aug. 1966 *G. B. Rossbach 6526* (ACAD). Washington Co., N. Lubec 26 Aug. 1964 *R. B. Pike & R. Burns s.n.* (NHA); Topsfield (in part) 7 Sept. 1957 *W. G. Dore 16992* (DAO).

New Brunswick

Charlotte Co., Anderson settlement 29 Sept. 1963 *W. A. Squires s.n.* (DAO). Sunbury Co., Blissville 11 Aug. 1962 *D. S. Christie 507* (DAO).

Ontario

Grenville Co., Kemptville 30 Aug. 1969 *C. & E. Frankton 2140* (DAO).

Québec

Châteauguay Co., Saint Chrysostome 20 Sept. 1954 *E. Rouleau 5476* (MT). Frontenac Co., St. Gédéon 9 Sept. 1959 *M. Raymond 59010* (MT). Huntingdon Co., Covey Hill 19 July 1951 *L. M. Terrill 6552* (MTMG); Hemmingford 9 Aug. 1951 *L. Cinq-Mars & A. Dion s.n.* (DAO, MT); Hemmingford 20 Aug. 1952 *I. Bassett & A. Hamel 2650* (DAO). Missisquoi Co., Missisquoi Bay, Pickle Point 19 Aug. 1953 *Fr. Louis-Alphonse 3973* (MT). Napierville Co., Sherrington 28 July 1951 *L. Cinq-Mars s.n.* (DAO, MT). Saint Jean Co., Lacolle 2 Sept. 1951 *M. Raymond & L. Cinq-Mars 1524* (DAO, MT); Lacolle 23 Aug. 1951 *L. Cinq-Mars s.n.* (DAO, MT); Lacolle 12 Aug. 1952 *I. Bassett & A. Hamel 2472* (DAO); Saint Valentin 29 Aug. 1963 *L. Cinq-Mars 63-1358* (DAO); Saint Valentin 8 Aug. 1952 *P. Louis-Marie 52666* (CAN, DAO, SFS). Wolfe Co., Lac Aylmer, W. Batoche 1 Sept. 1967 *S. Brisson & C. Hamel 13172* (MT).

1971–present

New Brunswick

Charlotte Co., Campobello Island 15 Aug. 1973 *P. Yeo, A. R. Hodgdon & R. B. Pike 20231* (NHA); New River Beach between Saint George and Saint John 5 Sept. 1976 *J. McNeill 5202* (OTT); Saint Croix River, Milltown hydrodam 26 Aug. 1985 *H. R. Hinds & M. Lulham 7938* (CAN).

Ontario

Carleton Co., Nepean 30 Sept. 1981 *D. F. Brunton & C. Frankton 3418A* (CAN); Nepean 30 Sept. 1981 *D. F. Brunton 3462* (CAN); Baxter Conservation Centre 1 Oct. 1980 *J. M. Gillett 18640* (CAN); Baxter Conservation Centre 12 Aug. 1979 *C. & E. Frankton 2508* (DAO); Grenville Co., Cardinal 6 Aug. 1986 *M. J. Shchepanek & A. W. Dugal 7228* (CAN). Manitoulin District, Manitoulin Island, Carrol Wood Bay 16 July 1976 *J. K. Morton & J. M. Venn NA9265* (SFS); Manitoulin Island, 1 km N. Hwy. 40 on road E. of Maple Lake 18 Aug. 1981 *D. F. Brunton 3305* (CAN). Nipissing District, Algonquin Prov. Park 8 Sept. 1985 *D. F. Brunton 6488* (DAO). Ottawa-Carleton Reg. Municip., S. W. Malakoff 8 Sept. 1976 *A. Hanes & J. Reddoch s.n.* (CAN); S. W. Malakoff 22 Aug. 1976 *A. & J. Reddoch s.n.* (CAN); S. Bell's Corners 20 Aug. 1977 *J. & A. Reddoch s.n.* (CAN); Bell's Corners 18 Aug. 1977 *C. & E. Frankton 2452* (DAO); Bell's Corners 23 Aug. 1977 *C. & E. Frankton 2453* (DAO); Bridlewood 3 Sept. 1977 *A. & J. Reddoch s.n.* (CAN); S. W. Bell's Corners 8 Sept. 1979 *D. R. Brunton, C. & E. Frankton 1983* (CAN); S. Cedar Grove picnic site 29 Aug. 1982 *S. J. Darbyshire & S. O'Donnell 1723* (CAN); Bell's Corners, Stoney Swamp 17 Sept. 1986 *J. McNeill s.n.* (OTT).

Québec

Gaspé-Est. Co., York Centre 14 Aug. 1972 *L. Cinq-Mars L197* (CAN, SFS); Forillon National Park, Cap-des-Rosiers 1 Sept. 1972 *M. M. Grandtner G1672* (CAN). Gatineau Co., Gatineau Park between Kelly and Glynn Lakes 12 Sept. 1976 *J. M. Gillett 17194* (CAN); Gatineau Park, S. Old Chelsea 4 Sept. 1980 *J. & A. Reddoch 238* (CAN); Gatineau Park, McKlosky Road Trail at Meach Lake 5 Aug. 1985 *D. S. Katz 318* (OTT). Île de Montréal, Outremont 8 Sept. 1982 *M. St. Pierre 11* (MTMG). Pontiac Co., N. Danford Lake 9 Sept. 1975 *M. J. Shchepanek & A. Dugal 1421* (CAN); Otter Lake, Yate's Uranium Mine 4 Sept. 1983 *A. Vogg 336* (CAN); Kent Lake 3 Sept. 1971 *W. G. Dore, M. Camfield & R. F. Dore 24910* (DAO). Terrebonne Co., Saint Sauveur-des-Monts 17 Aug. 1976 *Y. Pérusse 76388* (SFS); Sainte Thérèse 23 Sept. 1983 *B. Landry s.n.* (MT).

DISCUSSION

Euphrasia seems to have attracted little notice in American botany until the beginning of the 20th century when Wettstein (1896) wrote his monograph of the genus. Prior to this time, the few specimens which were available were treated as *E. officinalis* L. or varieties of it. Distributed throughout most of continental Europe (Yeo, 1978), *E. stricta* has been reported to have been introduced into New England near the turn of the century from whence it acted as a colonizing weed and spread rapidly (Fernald and Wiegand, 1915; Gleason, 1952). *Euphrasia stricta* has been repeatedly reported as "a recent introduction" or "possibly introduced" and as "following the progress of civilization." It is typically found in fields and lawns, by roadsides, and in other somewhat artificial habitats

associated with civilization, and has every appearance of an introduced plant. The earliest record of collection was in 1890 when plants were collected in Maine (Fernald and Wiegand, 1915). *Euphrasia stricta* was probably introduced into eastern Maine and eastern Canada by early European colonists during the 18th or 19th centuries, and has subsequently migrated northward and westward. It now appears to be well-established in eastern Ontario, particularly in the Regional Municipality of Ottawa-Carleton and vicinity. Recent collections from Manitoulin Island and Algonquin Provincial Park further attest to its rapid expansion westward.

ACKNOWLEDGMENTS

We gratefully acknowledge financial support from the Natural Sciences and Engineering Research Council of Canada, and thank the curators of the herbaria who lent us specimens. We also thank Deborah S. Katz-Downie and Andrée Quintin for assistance in the field, and Martin Dubé, Alison Dibble, Charles D. Richards and Sally C. Rooney for supplying additional plant material.

LITERATURE CITED

Downie, S. R., A. Quintin and J. McNeill. 1987. Le statut d'*Euphrasia borealis, E. nemorosa* et *E. stricta* dans l'est de l'Amérique du Nord: une analyse numérique. Canad. J. Bot. (in press).

Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed. (reprinted by D. Van Nostrand Co., New York 1970).

Fernald, M. L. and K. M. Wiegand. 1915. The genus *Euphrasia* in North America. Rhodora 17: 181–201.

Gleason, H. A. 1952. *Euphrasia, In:* The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada, Vol. 3., pp. 246–248. (reprinted by Hafner Publishing Co. Inc., New York 1968).

_____ and A. Cronquist. 1953. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Willard Grant Press, Boston.

Karlsson, T. 1976. *Euphrasia* in Sweden: hybridization, parallelism, and species concept. Bot. Not. 129: 49–60.

_____. 1984. Early-flowering taxa of *Euphrasia* (Scrophulariaceae) on Gotland, Sweden. Nord. J. Bot. 4: 303–326.

_____. 1986. The evolutionary situation of *Euphrasia* in Sweden. *In:* Biosystematics of the Nordic flora. B. &. J. Jonsell, Eds., Acta Univ. Ups., Symb. Bot. Ups. XXVII: 2, 61–71. Uppsala.

Marie-Victorin, Frère. 1964. Flore Laurentienne, 2nd ed. Revised by E. Rouleau. University of Montreal Press, Montreal.

Sell, P. D. and P. F. Yeo. 1970. A revision of the North American species of *Euphrasia* L. (Scrophulariaceae). J. Linn. Soc., Bot. 63: 189–233.

WETTSTEIN, R. VON. 1896. Monographie der Gattung *Euphrasia*. Leipzig.
YEO, P. F. 1978. A taxonomic review of *Euphrasia* in Europe. J. Linn. Soc., Bot. 77: 223–334.

S. R. D.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF OTTAWA
OTTAWA, ONTARIO K1N 6N5
CANADA

J. M.
REGIUS KEEPER
ROYAL BOTANIC GARDEN
EDINBURGH, SCOTLAND EH3 5LR
UNITED KINGDOM

RHODORA, Vol. 90, No. 863, 1988

REPRODUCTIVE BIOLOGY OF TWO SYMPATRIC SPECIES OF *CHIMAPHILA*

LISA A. STANDLEY, SARAH S. -H. KIM, AND INGRID M. HJERSTED

ABSTRACT

Sympatric populations of *Chimaphila maculata* and *C. umbellata* exhibit sequential flowering at a study site in Massachusetts. Each shows a positively skewed flowering curve typical of species with a synchronous onset of flowering. Although *Bombus bimaculatus*, *B. perplexus*, and *B. vagans* visit both species of *Chimaphila*, differences in pollinator preference may prevent interspecific pollen transfer during a short overlap in flowering time. These differences in phenology and pollinators are sufficient to prevent interbreeding, as experimental hybridizations show that the two species are fully interfertile.

Key Words: Chimaphila, Pyrolaceae, reproductive isolation, phenology, pollinators, competition, Bombus, Massachusetts

Chimaphila umbellata Bart. and *C. maculata* (L.) Pursh (Pyrolaceae) are sympatric in the understory of deciduous forests in eastern North America, and appear to be reproductively isolated. Despite similar floral morphologies and chromosome numbers (Copeland, 1947; Fernald, 1950; Löve, 1954) no hybrids or intermediate forms have been reported. This study was initiated to determine whether sympatric populations of *Chimaphila umbellata* and *C. maculata* differ in patterns of flowering phenology or pollinators, or whether reproductive isolation between these two species is due to post-pollination mechanisms.

Reproductive isolation in plants may be due to one of several pre- or post-pollination mechanisms. Many pairs of congeners utilize the same guild of pollinators but flower sequentially (Adams, 1983; Fleming, 1985; Haddock and Chaplin, 1982; Hurlburt, 1970; Kallunki, 1981; Reader, 1975; Stiles, 1975). This displacement of flowering times is generally assumed to be the outcome of competitive interactions among species with similar floral morphologies in which simultaneous flowering reduces fitness (Rathke and Lacey, 1985; Waser, 1983). Plants utilizing the same, limited pollinators may have limited pollination (resource competition) or shared pollinators may result in loss of gametes and reduced stigma function if pollinators are not limiting (interference competition). Pre-pollination barriers to interbreeding are assumed to have evolved

more frequently than post-pollination mechanisms, as the latter also prevents interbreeding but results in interference competition and reduction of fitness (Rathke, 1983; Waser, 1983). Although character displacement in floral morphology has clearly been shown to result from competition (Armbruster, 1985; Whalen, 1978), this causal relationship has not been unequivocably established for sequential flowering. Establishment of the mechanism of reproductive isolation in *Chimaphila* and identification of potential competitive interactions among species may provide a model for generating further hypotheses regarding the evolution of flowering patterns among sympatric species.

MATERIALS AND METHODS

Chimaphila is a northern hemisphere genus with 8 species of rhizomatous evergreen subshrubs (Airy-Shaw, 1973), two of which occur in eastern North America. *Chimaphila umbellata*, a circumboreal species, is found from Wisconsin to Nova Scotia and south to Georgia. *Chimaphila maculata* occurs from Ontario to Massachusetts and south to Georgia (Fernald, 1950). Large clones may be formed by growth of the sympodial rhizomes, which produce erect ramets (shoots), each bearing several whorls of leaves and a terminal raceme of 1–7 actinomorphic, polypetalous flowers. The two species differ in leaf and flower color and in flower number. *Chimaphila umbellata* has glossy green leaves and 2–7 pink flowers, while *Chimaphila maculata* has dark green leaves with white markings, and 1–3 white flowers (Fernald, 1950). Flowers in both species are inverted and borne at a 45° angle to the peduncle. The waxy petals are initally involute and imbricate, enclosing the stamens and gynoecium, but reflex completely during a 4-day period. The single pistil has a large, sessile, sticky stigma. The 10 stamens each consist of a filament that is attached to the middle of the anther and that has large paired basal flaps, and an anther that dehisces through terminal pores. In bud, the anthers are inverted with the pores directed toward the base of the flower, but during the first 4 days of flowering they gradually rotate 180°. Petals and anthers generally wither and abscise within 5–6 days of opening. Observations of flowering times and pollinators were made in 1983 and 1986 for both *Chimaphila umbellata* and *C. maculata*. These populations occur sympatrically in an area of ca. 5 ha on the W slope of a

wooded drumlin on the Wellesley College campus (Massachusetts, Norfolk Co., Wellesley, 0.6 km SW of the junction of state Rts 135 & 16, USGS Natick Quadrangle, approx. 42° 17′ 30″ N, 71° 16′ W). The overstory at this site consists of *Quercus alba* L., *Q. borealis* Michx. f., *Carya glabra* (Mill.) Sweet, *C. ovata* (Mill.) Koch, *Acer rubrum* L., *Pinus strobus* L., and numerous small stump sprouts of *Castanea dentata* (Marsh.) Borkh. The understory is dominated by ericaceous shrubs including *Vaccinium angustifolium* Ait., *Kalmia latifolia* L., *K. angustifolia* L., *Gaylussacia baccata* (Wang.) Koch, *Viburnum lentago* L. and *V. acerifolium* L. The sparse herbaceous stratum consists of *Pteridium aquilinum* (L.) Kuhn, *Maianthemum canadense* Desf., *Cypripedium acaule* Ait., *Uvularia sessilifolia* L., *Pyrola americana* Sweet, *Monotropa uniflora* L., and *Gaultheria procumbens* L. Soil pH values range from 4.2 to 4.6.

All groups of contiguous ramets of each species were located and numbered. These clumps are assumed to be equivalent to clones, but have not been excavated to test this assumption. For *Chimaphila umbellata*, there were 22 clumps ranging in size from 25 1200 ramets (X = 300), and for *C. maculata* there were 79 clumps ranging in size from 1–90 ramets (X = 16). No microsite differences were observed among clumps of the two species, which were frequently intermixed. In 1983, the three largest clumps of each species were arbitrarily chosen for study. In 1986, the four largest clumps of *C. umbellata* and five largest clumps of *C. maculata* were selected in order to provide a sample of 200 flowering ramets of *C. umbellata* and 100 flowering ramets of *C. maculata*. All flowering ramets in each selected clump were marked and numbered. For each species, we selected clumps from the top, middle, and base of the slope in order to eliminate any bias due to topographic differences in phenology.

We enclosed ramets used for pollination experiments in 10″ long tubes of nylon mesh to exclude insects in 1987. Inflorescences were pruned so that only one flower remained on a ramet to exclude the possibility of geitonogamy due to occasional ant visitors. Buds were emasculated prior to opening, and pollen was collected from the excised anthers. Pollen from all individuals of a species was pooled and stored at 45° F. For pollination, stigmas were dipped into pollen placed in a glass depression slide. For each species, 25% of the available buds were not pollinated, 25% were pollinated with

conspecific pollen, and 50% were used for interspecific crosses. Final sample sizes are reduced in some treatments due to disturbance or accidental loss of flowers. Pollination success was determined by scoring each pistil three months after pollination as either fruiting (an enlarged ovary containing seeds) or aborted (the ovary did not enlarge significantly, and seeds were not produced). Five unmanipulated flowering ramets of each species were also enclosed in aluminum screen cages to determine whether autogamy can occur without insect transfer of pollen.

During the flowering period, all marked ramets were examined daily and the numbers of buds, open flowers, and fruits were recorded. Flowers were recorded as open during the period between the time when the stigma and anthers were first visible until the petals began to wither and abscise. Pollinators were observed for a total of 11 hours in 1983 and 45.5 hours in 1986. Floral visitors were captured for identification, and observations were made on the behavior of pollinators within the clump.

The method of Estabrook et al. (1982) was used to provide a statistical test of the separation in flowering times between the two species. This procedure is a non-parametric test of the null hypothesis that any floral bud of either species has an equal probability of opening on any day, and is based on the magnitude of the largest difference in cumulative frequencies of open buds. This difference is compared to a calculated threshold value, T, which has a defined probability of occurrence.

RESULTS

Interfertility

Chimaphila umbellata and *C. maculata* are fully interfertile in reciprocal crosses. Fruit sets of 74.6% were obtained with *C. umbellata* as the seed parent and 92.5% with *C. maculata* as the seed parent. For each species, chi-square tests showed significant differences between observed and expected (50%) values for successful and unsuccessful pollination (Table 1). These results are comparable with those obtained in conspecific crosses. Neither species is capable of apomixis, although only the sample size for *Chimaphila umbellata* was large enough to obtain a significant result in a chi-square test of difference between observed and expected (50%) fruit set (Table 1). Although a low fruit set occurred in some of the unpolli-

Table 1. Results of experimental pollinations between two *Chimaphila* species.

Treatment	*C. umbellata* Number of Flowers			*C. maculata* Number of Flowers		
	Fruited	Aborted	Total	Fruited	Aborted	Total
No pollination	1	45	46*	5	13	18
Conspecific	44	3	47*	10	1	11
Interspecific	82	28	119*	49	4	53*

*X^2 significant, p 0.005.

nated plants, pollen was found on these stigmas and fruiting is assumed to be due to accidental pollination. None of the flowers on caged plants set fruit, indicating that insect visitation is required for pollination.

Phenology

Initiation of flowering was not observed in *Chimaphila umbellata* in 1983, but occurred between June 26, when no open flowers were observed, and June 29. Flowering began several days earlier in 1986 (Figure 1). In 1983, a maximum of 56% open flowers was reached 3–5 days after the onset of flowering, but in 1986 a lower maximum of 45% occurred after 9 days. The curves for both years are slightly positively skewed, with a steeper inital slope and a tail at the end of the flowering period. The flowering period in 1983, excluding the tail, was 14 days. Over 90% of the bud population was open by day 7. The flowering period in 1986 was 22 days, and 12 days elapsed before 90% of the bud population had opened. The difference between years may be due to weather, but may also be the result of asynchrony among clumps. In 1983, one of the three clumps sampled reached its maximum flowering 5 days after the other two, and in 1986 the additional fourth clump was delayed by 8–10 days relative to the other three. This asynchrony may also explain the relatively low proportion of the total bud population open at peak bloom.

Chimaphila maculata had remarkably similar flowering curves for the two years. Flowering began on July 7 in both years (Figure 1). In 1983, a maximum of 74% open flowers was reached 9 days after the onset of flowering, while in 1986 a peak of 73.5 % occurred after 10 days. Over 90% of the buds had opened within 9 days in both 1983 and 1986. Flowering curves are also positively skewed in this species, but differences were noted between years in the de-

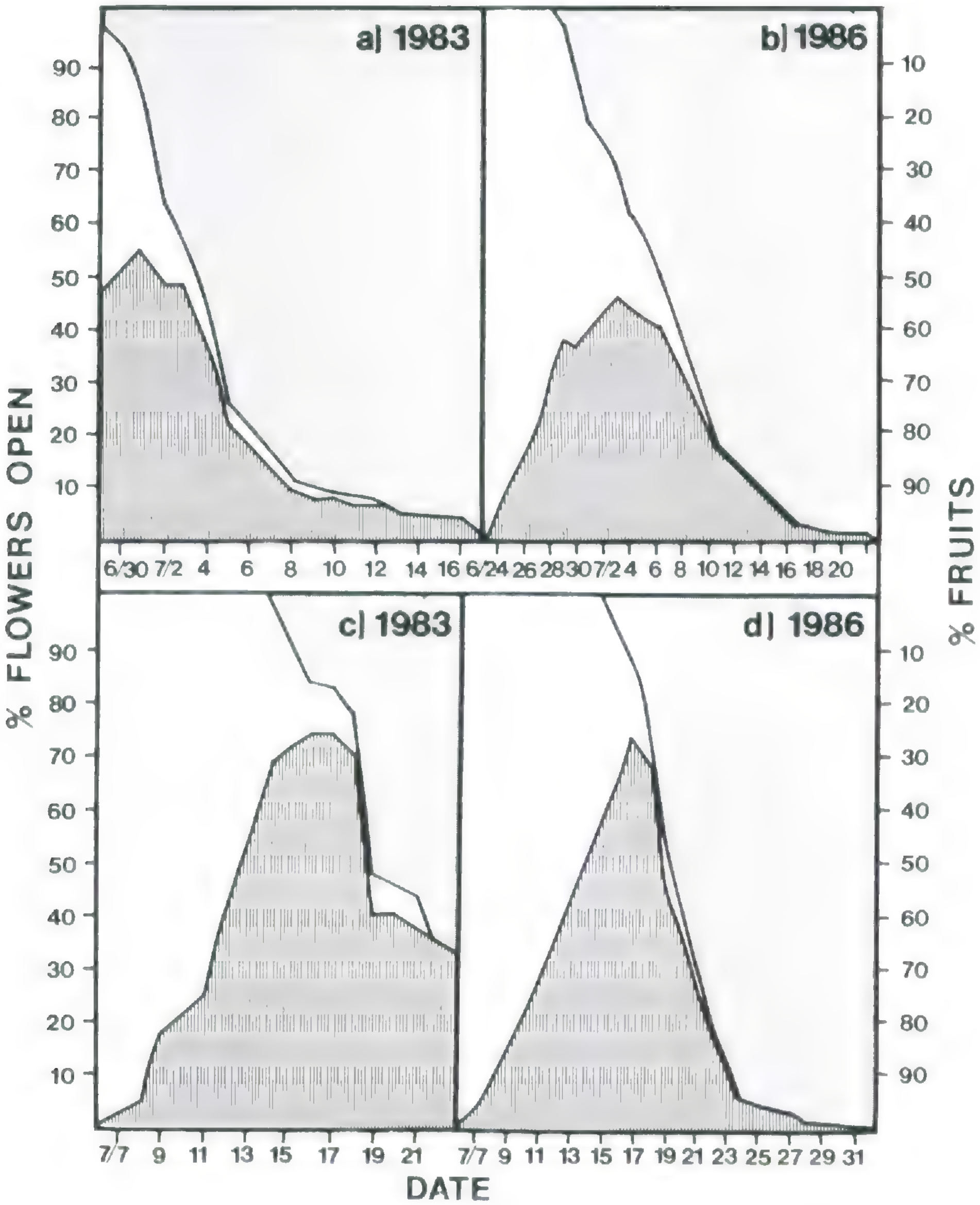


Figure 1. Cumulative flowering and fruiting curves for *Chimaphila umbellata*: **a.** 1983, **b.** 1986; for *C. maculata*: **c.** 1983, **d.** 1986. Vertical bars indicate the percent of total bud population present as open flowers; shading indicates percent of total bud population present as fruits.

scending portion of the curves. In 1983, the proportion of open flowers initially decreased rapidly over two days to 40%, and subsequently decreased more gradually. In 1986, the decrease was uniformly linear with a slope of ca 10% per day with a small number of persistent flowers, similar to the tail described for *C. umbellata*. The

flowering period of *C. maculata* extended for 17–20 days in both years, excluding the tail.

Flowers that opened early in the flowering period had lost petals and initiated fruit development 4 5 days after buds opened, but flowers that opened late in the blooming period remained open for as long as 10–12 days without petal abcission or fruit development. Unpollinated flowers that were caged to exclude insects remained open for 10–12 days before withering, suggesting that late-opening flowers may persist due to lack of pollination. The negative tails on the flowering curves of both species consist of these persistent flowers, rather than newly-opened buds.

Although *Chimaphila maculata* began flowering later than *C. umbellata* by 9 days in 1983 and 13 days in 1986, the difference between the dates of peak flowering was 15 days in 1983 and 14 days in 1986 (Figure 2). Estabrook's test shows that the phenologies of the two species were significantly different in both years ($T = 0.154$ in 1983; $T = 0.1002$ in 1986. Both values are significant at $p = 0.05$). Although the flowering periods overlapped for 11 days in 1983 and 15 days in 1986 (Figure 2), the numbers of open flowers of *Chimaphila umbellata* were low (less than 10%) during these periods.

Pollinators

The principal pollinators of both species of *Chimaphila* are bumblebees (*Bombus* spp.), although *C. maculata* is also rarely visited by honeybees, *Apis mellifera* (Table 2). *Chimaphila umbellata* was visited by workers of *Bombus bimaculatus*, *B. vagans*, and *B. perplexus*. *Bombus bimaculatus* and *B. vagans* were the most frequent pollinators in both years, and *Bombus perplexus* did not visit *C. umbellata* in 1986. *Chimaphila maculata* was visited primarily by workers and males of *Bombus perplexus*, although *B. bimaculatus* and *B. vagans* were also occasionally observed. Although the two species of *Chimaphila* utilize the same guild of pollinators, *C. umbellata* is pollinated primarily by *Bombus bimaculatus* and *B. vagans*, while *C. maculata* is pollinated by *B. perplexus*.

Rates of bee visitation were low, and differed more between years than between species. For *Chimaphila maculata* and *C. umbellata*, an average of 3.2 and 2.9 bees per hour visited each species in 1983, while rates of only 0.65 and 0.57 were observed in 1986 (Table 2). Bees tended to land at the periphery of a clump and visit all open flowers for ca. 4 seconds per flower. As tests indicate that Chimaphila species are self-compatible but not self-pollinating nor apo-

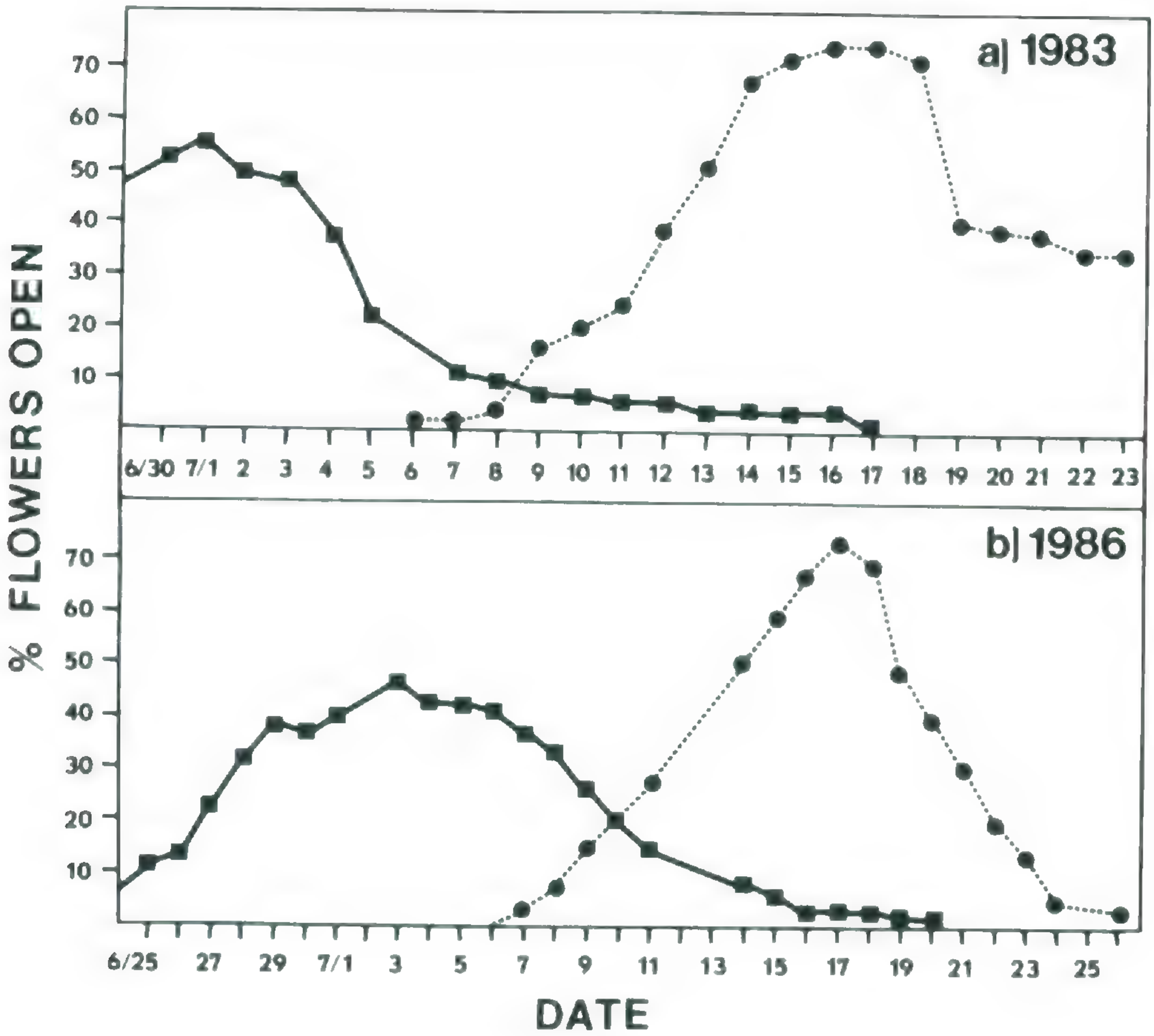


Figure 2. Flowering curves for *Chimaphila umbellata* (solid line with square dots) and for *C. maculata* (dashed line and round dots): **a.** 1983 and **b.** 1986. The curves indicate percent of total bud population present as open flowers on each date sampled.

mictic, this pattern of pollinator movement provides considerable opportunity for geitonogamy.

Bees did not buzz flowers of either *Chimaphila umbellata* or *C. maculata* to remove pollen. Rather, they probed around the base of the gynoecium and beneath the staminal flaps, apparently collecting nectar. Only 2 of the 38 bees collected had *Chimaphila* pollen packed in their corbiculae.

DISCUSSION

Reproductive isolation of *Chimaphila umbellata* and *C. maculata* in Massachusetts appears to be primarily due to differences in flowering phenology, as results show that these species share pollinators and do not exhibit different microsite preferences. Sequential flow-

Table 2. Insect visitors of *Chimaphila maculata* and *C. umbellata*.[1]

	C. maculata				*C. umbellata*			
	1983		1986		1983		1986	
	N	%	N	%	N	%	N	%
Bombus bimaculatus	0	1	7	1	10	5	71	
Bombus vagans	2	29	1	7	5	50	2	29
Bombus perplexus	4	14	12	86	4	40	0	0
Apis mellifera	1	14	0	0	0	0	0	0
Total	7		14		10		7	
Hours of observation	5	24.5		6.25		21		
Total insect visits[2]	16		16		18		12	
Average visitation rate (insects/hr)	3.2		0.65		2.9		0.57	

[1]Figures represent insects collected and identified.
[2]Other insect visitors observed and tentatively identified but not collected for *C. maculata: Bombus vagans* (4), *B. perplexus* (3), and *Apis mellifera* (2) in 1983, *B. perplexus* (1) and *Apis mellifera* (1) in 1986; for *C. umbellata: B. bimaculatus* (1), *B. vagans* (2) and *B. perplexus* (5) in 1983, *B. bimaculatus* (2) and *B. vagans* (3) in 1986.

ering may also operate as an isolating mechanism among other sympatric pairs of *Chimaphila* species. Observations on *Chimaphila umbellata* and *C. menziesii* (R. Br.) Spreng., a close relative of *C. maculata*, in the Cascade Mountains in Washington showed that these also flowered sequentially at the same site with a difference in peak flowering times of 14 days, but with *C. menziesii* flowering earlier (8 July) and *C. umbellata* flowering later (22 July) (Standley, unpubl. data, 1982). Such sequential flowering times are common among sympatric, related species and are presumed to result from character displacement due to decreased fitness of synchronously flowering congeners (Adams, 1983; Armbruster and Herzig, 1984; Haddock and Chaplin, 1982; Kallunki, 1981; Reader, 1975; Stiles, 1975).

Interference competition may reduce conspecific pollen donation or seed set or may produce infertile hybrids, while resource competition may reduce rates of floral visitation (Campbell and Motten, 1985; Motten, 1986; Rathke, 1983; Waser, 1978; 1983). Our results do not allow us to test these hypotheses, nor to answer the more fundamental question of whether sequential flowering in *Chimaphila umbellata* and *C. maculata* is due to character displacement or simply to different responses to environmental cues. Determination of the length and shape of the flowering curves of populations of *Chimaphila umbellata* north of the range of *C. maculata* may reveal

whether competitive interactions have compressed or displaced its flowering times. Heinrich (1976a) estimated the flowering period of *Chimaphila umbellata* in Maine as 14 days, which suggests that flowering curves have not been compressed. Additional studies of sympatric populations, and establishment of transplant populations may permit these hypotheses to be tested.

Reproductive isolation may also be enforced by differences in pollinators. The same three species of *Bombus* pollinate both species of *Chimaphila*, although *C. umbellata* was primarily visited by *Bombus bimaculatus*, and *C. maculata* by *B. perplexus*. *Bombus vagans* visited both species, with a slight preference for *C. umbellata*. Shared pollinator species do not necessarily indicate that interspecific pollen transfer occurs, as individual bees may display a consistent preference for a particular species or clump (Adams, 1983; Heinrich, 1976b; 1979). Studies of *Bombus* have shown that individual bees rarely visit more than one plant species (Kwak and Jennersten, 1987; Teräs, 1987) and that individuals of subgenus *Pyrobombus*, which includes both *B. vagans* and *B. bimaculatus*, are least likely to switch (Teräs, 1987). Optimal foraging theory (Pyke et al., 1977) would also predict that pollinators would switch to the more abundant floral resource, and would cease to visit the few open flowers of *Chimaphila umbellata* when *C. maculata* was available. The persistence of unpollinated flowers of *Chimaphila umbellata* during the peak flowering of *C. maculata* provides support for this conclusion. Further observation of pollinator behavior and movement, as well as the dispersal of labeled pollen, would provide more definitive answers regarding the potential for interspecific pollen transfer.

Observations made in this study do not support Buchman's report (1983) that *Chimaphila umbellata* is buzz pollinated. The absence of pollen in the corbiculae indicates that *Bombus* species utilize *Chimaphila* as a nectar, rather than a pollen, source. Floral morphology of *Chimaphila* does not entirely fit Buchmann's model for buzz pollination. Although these species do have actinomorphic, pendant flowers and poricidal anthers, the anthers are neither brightly colored nor organized into a cone around a slender style. Studies of nectar production are necessary in order to test this hypothesis.

Despite interfertility, *Chimaphila umbellata* and *C. maculata* in Massachusetts do not interbreed. Differences in phenology and pollinators appear to prevent interspecific pollen transfer, although inviability of hybrid seed has not been eliminated as a possible

additional post-pollination isolating mechanism. These differences are assumed to have evolved through competition and character displacement, but further research is needed to test hypotheses regarding evolution of isolating mechanisms.

ACKNOWLEDGMENTS

We are grateful to M. A. Schlessman and two anonymous reviewers for comments on this manuscript, and especially to C. Voigt for identification of bees. Research was supported in part by Brachman Hoffman grants in 1986 and 1987.

LITERATURE CITED

Adams, V. D. 1983. Temporal patterning of blooming phenology in *Pedicularis* on Mount Rainier. Canad. J. Bot. 61:786–791.

Airy-Shaw, H. K. 1973. A Dictionary of the Flowering Plants and Ferns. Cambridge Univ. Press., Cambridge.

Armbruster, W. S. 1985. Patterns of character divergence and the evolution of reproductive ecotypes of *Dalechampia scandens* (Euphorbiaceae). Evolution 39: 733–752.

_____ and A. L. Herzig. 1984. Partitioning and sharing of pollinators by four sympatric species of *Dalechampia* (Euphorbiaceae): are natural assemblages "random" or organized? Ann. Missouri Bot. Gard. 71: 1–16.

Buchmann, S. L. 1983. Buzz pollination in angiosperms. *In*: C.E. Jones and R.J. Little, Eds., Handbook of Experimental Pollination Biology pp. 73–113. Van Nostrand Reinhold, New York.

Campbell, D. R. and A. F. Motten. 1985. The mechanism of competition for pollination between two forest herbs. Ecology 66: 554–563.

Copeland, H. F. 1947. Observations on the structure and classification of the Pyroleae. Madrono 9: 65–102.

Estabrook, G. F., J. A. Winsor, A. G. Stephenson, and H. F. Howe. 1982. When are two phenological patterns different? Bot. Gaz. (Crawfordsville) 143: 374–378.

Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed. (Corrected Printing, 1970). Van Nostrand, Reinhold, New York.

Fleming, T. H. 1985. Coexistence of five sympatric Piper (Piperaceae) species in a tropical dry forest. Ecology 66: 688–700.

Haddock, R. C. and S. J. Chaplin. 1982. Pollination and seed production in two phenologically divergent prairie legumes (*Baptisia leucophora* and *B. leucantha*). Amer. Midl. Naturalist 108:175–186.

Heinrich, B. 1976a. Flowering phenologies: bog, woodland, and disturbed habitats. Ecology 57:890–899.

_____. 1976b. The foraging specializations of individual bumblebees. Ecol. Monogr. 46:105–128.

_____. 1979. "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. Ecology 60: 245–255.

HURLBURT, S. H. 1970. Flower number, flowering time, and reproductive isolation among ten species of *Solidago* (Compositae). Bull. Torrey Bot. Club 97:137–187.

KALLUNKI, J. A. 1981. Reproductive biology of mixed-species populations of *Goodyera* (Orchidaceae) in northern Michigan. Brittonia 33:137–155.

KWAK, M. M. AND O. JENNERSTEN. 1987. Competition for bumblebee visitation between two simultaneously flowering plant species and its consequences. XIV International Botanical Congress Abstracts p. 374.

LÖVE, A. 1954. Cytotaxonomic evaluation of corresponding taxa. Vegetatio 5: 212–224.

MOTTEN, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecol. Monogr. 56: 21–42.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137–154.

RATHKE, B. 1983. Competition and facilitation among plants for pollination. *In:* L. Real, Ed., Pollination Biology, pp. 305–329. Academic Press, New York.

———, AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. Annual Rev. Ecol. Syst. 16:179–214.

READER, R. J. 1975. Competitive relationships of some bog ericads for major insect pollinators. Canad. J. Bot. 53:1300–1305.

STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56 :285–301.

TERÄS, I. 1987. Bumblebees visiting more than one plant species. XIV International Botanical Congress Abstracts, p. 374.

WASER, N. M. 1978. Interspecific pollen transfer and competition betweem co-occurring plant species. Oecologia 36:223–236.

———. 1983. Competition for pollination and floral character differences among sympatric plant species: a review of evidence. *In:* C. E. Jones and R. J. Little, Eds., Handbook of Experimental Pollination Biology, pp. 277–293. Van Nostrand Reinhold, New York.

WHALEN, M. D. 1978. Reproductive character displacement and floral diversity in *Solanum* section *Androceras*. Syst. Bot. 3: 77–86.

DEPARTMENT OF BIOLOGICAL SCIENCES
WELLESLEY COLLEGE
WELLESLEY, MA 02181

RHODORA, Vol. 90, No. 863, 1988

TAXONOMY OF *ARNICA* (ASTERACEAE) SUBGENUS *ARCTICA*[1]

STEPHEN R. DOWNIE AND KEITH E. DENFORD

ABSTRACT

Evaluation of systematic relationships in *Arnica* subgenus *Arnica* show that the complex consists of seven species. No new taxa have been proposed; however, names of several previously recognized taxa are treated as synonyms. *Arnica augustifolia, A. frigida,* and *A. lonchophylla,* each consisting of two subspecies, are extremely polymorphic and variable in chromosome number. *Arnica louiseana, A. rydbergii, A. fulgens* and *A. sororia* are morphologically distinct. A taxonomic revision of the subgenus includes descriptions, keys, synonymies, distribution maps, and a discussion of phylogenetic relationships.

Key Words: Asteraceae, *Arnica* subgenus *Arctica,* taxonomy, phylogeny, phytogeography, Northern Hemisphere

INTRODUCTION

Arnica subgenus *Arctica* is composed of a number of polyploid, predominantly agamospermous taxa distributed throughout temperate and arctic regions in the northern hemisphere. These rhizomatous perennial herbs are characterized by simple or occasionally branched stems bearing large hemispheric to campanulate-turbinate capitula, and a white, barbellate pappus. The subgenus is confined to latitudes between 45° and 80° N. in North America and 60° and 80° in the U.S.S.R., with disjunct members in northern Scandinavia. Taxonomic treatments of this complex have been influenced by the morphological variability encountered, particularly within *A. angustifolia* Vahl, *A. frigida* Meyer ex Iljin and *A. lonchophylla* Greene.

The basic chromosome number for *Arnica* is undoubtedly $x = 19$ (Böcher and Larsen, 1950; Orndduff et al., 1967; Downie, 1985), with cytotypes $2n = 38$, 57, 76, and 95 reported for *Arnica angustifolia* and *A. frigida,* $2n = 38$, 57, and 76 for *A. lonchophylla,* $2n = 76$ and 95 for *A. louiseana,* $2n = 38$ and 76 for *A. rydbergii,* and $2n = 38$ for both *A. fulgens* and *A. sororia* (Downie, 1987; Ph.D. dissertation,

[1]Based on a dissertation submitted to the Department of Botany, University of Alberta, by S. R. D. in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

U. of Alberta, Edmonton). All previously reported chromosome counts for subgenus *Arctica* have been presented elsewhere (Downie, 1987; Ph.D. dissertation, U. of Alberta, Edmonton). Amphimictic ($2n = 38$) species of subgenus *Arctica* are closely correlated with non-glaciated regions; apomictic ($2n = 57$, 76, and 95) phases are largely responsible for the recolonization of previously glaciated areas [Barker (1966; Ph.D. dissertation, U. of Wash., Seattle); Downie and Denford, 1986a; Downie, 1988].

Investigations of flavonoid constituents in *Arnica angustifolia* (Downie, 1988), *A. frigida* (Downie and Denford, 1986b), and *A. lonchophylla* (Downie and Denford, 1988) indicate extreme variability within taxa and a high similarity between taxa, and offer little of taxonomic value. In subgenus *Arctica,* flavonoid diversity appears to have accompanied high morphological variation. Flavonoid differences are apparent between *A. fulgens* and *A. sororia,* although populations of the two can be found with identical flavonoid chemistry (Downie and Denford, 1987). Only *A. louiseana* and *A. rydbergii* are clearly delimitable on the basis of their flavonoid chemistry (Downie and Denford, 1988).

Evaluation of systematic relationships in subgenus *Arctica* show that the complex, as circumscribed in this revision, consists of seven species, including six taxa ranked at the subspecific level. Names of seven taxa previously recognized by Maguire (1943) are treated as synonyms. This revision incorporates data from morphology, cytology, and flavonoid chemistry to elucidate the nomenclature and classification of the subgenus. This study is based on extensive field studies and collections from throughout the range of the complex and from an examination of approximately 2200 herbarium specimens (including types). A list of the herbarium specimens examined during the course of this investigation is on deposit at MO.

TAXONOMIC HISTORY

In the most recent monograph of *Arnica,* Maguire (1943) recognized 32 species in five subgenera, *Andropurpurea, Arctica, Austromontana, Chamissonis* and *Montana* and presented a comprehensive account of the taxonomic history of the subgenus. Subgenus *Austromontana* has recently been systematically investigated by Wolf and Denford (1984), who recognized nine species within the subgenus, reducing the number of taxa recognized by Maguire by four. Maguire's recognition of seven species and thirteen subspecies within subgenus *Arctica* was based primarily on an

examination of herbarium specimens. At that time, information on chromosome numbers and reproductive behavior within the genus was virtually unknown and resulted in a lack of knowledge of the morphological variation in these plants created by apomixis, polyploidy, and phenotypic plasticity.

In their revision of *Arnica* for North American Flora, Ediger and Barkley (1978) essentially adopted Maguire's (1943) treatment of subgenus *Arctica,* recognizing six species and seven varieties. *Arnica plantaginea* Pursh was combined with *A. alpina* subsp. *sornborgeri* (Fern.) Maguire, and the assemblage treated as *A. alpina* var. *plantaginea* (Pursh) Ediger & Barkl. The infraspecific taxa of *A. lonchophylla* were not recognized. At the same time, Douglas and Ruyle-Douglas (1978) treated *A. lonchophylla* as a subspecies of *A. angustifolia,* and *A. sororia* as a variety of *A. fulgens.*

MORPHOLOGY AND TAXONOMIC CRITERIA

Barker (1966, Ph.D. dissertation, U. of Wash., Seattle) demonstrated that the major populations of *Arnica angustifolia, A. lonchophylla* and *A. frigida* are autonomously apomictic; that is, agamospermy (seed production) can proceed without the stimulus of pollen tubes or fertilization of the polar nuclei. One of the effects agamospermy has on plant populations is the formation of microspecies, restricted in distribution to relatively small geographical areas (Grant, 1971). The morphological variability encountered in *Arnica* is attributable to apomixis and polyploidy [Afzelius, 1936; Gustafsson, 1947; Barker (1966; Ph.D. dissertation, U. of Wash., Seattle)]. Accordingly, the perplexing morphological and chemical variability in *Arnica* subgenus *Arctica* is likely the result of microspecies formation via apomixis. Other factors contributing to the complex variation patterns in the subgenus include: (1) phenotypic plasticity, (2) hybridization and introgression (perhaps between *A. angustifolia* and *A. lonchophylla*), (3) pollinator non-specificity, (4) geographical and (5) ecological isolation (Downie, 1987; Ph.D. dissertation, U. of Alberta, Edmonton).

In the past, attempts to give taxonomic credence to every morphological variant, or anomalous individual, resulted in complicated and confusing treatments. As a result of this study, the total number of taxa in subgenus *Arctica* is reduced from seventeen to ten, with one new combination proposed. Three species recognized in this treatment, *Arnica angustifolia, A. frigida* and *A. lonchophylla,* exhibit variability in morphology, ploidy level and foliar

flavonoid chemistry (Downie, 1987; Ph.D. dissertation, U. of Alberta, Edmonton). This variation has no doubt influenced previous taxonomic treatments. Characters useful in distinguishing taxa are: the presence or absence of short stipitate-glands on the leaves, achenes and involucral bracts, the shape of the capitulum, petiole length, the type of leaf margin, and achene pubescence.

PHYLOGENY

The genus *Arnica* is clearly defined, with the included species held together by similar phytochemistry, chromosome base number and structural characters. It is monophyletic, being derived from a hypothesized ancestor, *Protoarnica* (Maguire, 1943). Maguire considered *Arnica* to have originated in the arctic and subarctic regions of western North America from whence it spread eastward, westward, and southward. The paucity of *Arnica* species in Europe and Asia, and the presence of about 25 species confined primarily to the arctic, boreal and montane regions of northwestern North America, was used as supporting evidence. Based upon principal centers of dispersal and morphological similarity, Maguire (1943) recognized five subgenera, with subgenus *Arctica* representing the most ancestral group. The probable relationships of other subgenera in *Arnica* are not at all clear, and precise delineation is speculative. These subgenera may have arisen from subgenus *Arctica,* or independently from *Protoarnica* (Maguire, 1943). Maguire's delineation of taxa within the subgenus is also highly speculative, with numerous alternative origins proposed for many of the taxa.

The prevalence of apomixis, polyploidy and hybridization in *Arnica* makes phylogenetic analysis, and sister group designation, for subgenus *Arctica* difficult. The taxa comprising the remaining four subgenera, all plausible sister groups, have been used as the outgroup in this study. Subgenus *Arctica* is also monophyletic. All species possess (1) a large, broadly hemispheric to campanulate-turbinate capitulum, (2) a white, barbellate pappus, (3) a rhizome covered with dark, imbricate scales and leafbase remnants, (4) arctic/alpine ecology (with the exceptions of *A. fulgens, A. sororia* and *A. lonchophylla*), and (5) the prevalence of simple flavonols and flavones based on the glycosides of glucose and galactose. Based upon an examination of structural, phytochemical, ecological and phytogeographical data, we agree with Maguire that *Arctica* represents the archetypal group, being derived from the postulated precursor, *Protoarnica.*

Arnica angustifolia has been interpreted as the progenitor of all taxa within the subgenus (Maguire, 1943), and we concur with this view. It is the most widespread and only completely circumpolar species of *Arnica.* This taxon also protrudes in a southerly direction along three major radii: (1) along the coast of eastern Siberia, (2) in the alpine regions of northwestern North America, and (3) along the North Atlantic coast in eastern North America. In these regions it is sympatric, or close to, all other arnicas. With four ploidy races (including relictual diploid populations in unglaciated Alaska-Yukon), a seemingly ancient and diverse flavonoid chemistry, an arctic-alpine ecology, a wide geographic distribution, a non-specific habitat preference, an extremely polymorphic habit, and the possession of many plesiomorphous morphological features, *A. angustifolia* is almost certainly the ancestral species in subgenus *Arctica,* and perhaps the entire genus.

Arnica frigida and *A. louiseana* are early derivatives of *A. angustifolia,* for they maintain similar plesiomorphous morphological and phytochemical features, and occur in the same geographic areas as *A. angustifolia.* Maguire (1943) stated that *A. frigida* became segregated into two outlying geographical races, subsp. *griscomii* in eastern Canada, and *A. louiseana* (or more likely a precursor to present-day *A. louiseana*) to the south. There appears to be little doubt of the close genetic affinity between *A. frigida* subsp. *frigida* and *A. frigida* subsp. *griscomii.* Both taxa are similar chemically and morphologically, but are distinguished by geographical distribution, habitat specificity, and a few subtle morphological differences (Downie and Denford, 1986a). *Arnica louiseana,* with its glandular leaves, stems, involucral bracts, periclinium and achenes, is distinctive. The lack of luteolin 7-O-glucoside in *A. frigida* and *A. louiseana,* a flavone prevalent in all other species, and similar morphological characters, are unifying features suggesting that these two taxa originated from a common ancestor.

With a habitat specificity to more xeric conditions, *Arnica fulgens* and *A. sororia* evolved from the more common arctic-alpine regions to prairie and grasslands habitats. The marked degree of morphological, cytological, ecological, and flavonoid similarity between *A. fulgens* and *A. sororia* suggests that they are sister groups. This is in contrast to Maguire's (1943) proposed phylogenetic interpretation, in which these two taxa were treated as unrelated. All collections of *A. fulgens* had luteolin 6-O-methoxy 7-O-glucoside and apigenin, whereas only two collections of *A. sororia* had these compounds.

The presence of these two flavonoids in *A. sororia* is significant; however, a more thorough examination to determine the full range of flavonoid variability throughout the entire distribution of these plants is required before phylogenies based on flavonoid data can be positively assured. In *A. fulgens,* the unique occurrences of dense axillary tufts of hair at the base of the stem, disc corollas with septate-glandless hair, the possibility of polyploidy (Taylor and Brockman, 1966), and luteolin 6-O-methoxy 7-O-glucoside and apigenin suggests that this taxon is best considered derived from *A. sororia.*

Arnica fulgens and *A. sororia* are morphologically more similar to *A. angustifolia* than to *A. lonchophylla.* The large, hemispheric capitulum, entire to irregularly denticulate or dentate leaves, and the short, narrow or broad-winged petioles of *A. fulgens, A. sororia,* and *A. angustifolia* are in contrast to the numerous campanulate-turbinate capitula, and the long-petiolate, regularly dentate leaves of *A. lonchophylla.*

Of somewhat greater divergence from the ancestral condition are *Arnica lonchophylla* and *A. rydbergii,* the latter representing the most patristic taxon within the subgenus. Sessile leaves, narrowly campanulate-turbinate capitula, minutely denticulate or entire ligulate florets, linear-oblong to narrowly lanceolate involucral bracts, and the presence of both quercetin 3, 7-O-diglucoside and kaempferol 6-O-methoxy 3-O-glucoside in *A. rydbergii* clearly sets this taxon off from the remainder of the subgenus. It still, however, retains all the features characteristic of subgenus *Arctica,* and definitely belongs within this complex.

TAXONOMIC TREATMENT

Arnica Linnaeus, Sp. Pl. 884. 1753. TYPE species: *Arnica montana* L.

Stems herbaceous, simple or branched, arising from a perennial rhizome; leaves 1–12 pairs, simple, opposite (or apparently all basal), sessile or narrowly to broadly petiolate, the uppermost leaves sessile and reduced, rarely alternate; capitula solitary to many in a cymose inflorescence, radiate or discoid, broadly hemispheric to turbinate, the periclinium obvious; involucral bracts biseriate, or loosely uniseriate; receptacle convex, naked or with conspicuous tawny or stramineous hairs; ligulate florets pistillate, yellow to orange, the ligule entire or dentate; disc florets uniform, perfect, yellow to orange, tubular or goblet-shaped; anthers yellow or pur-

ple, the base minutely auriculate; styles exserted, bifurcate, revolutely coiled, the tip somewhat broadened and truncate, the outer surface papillose; achenes cylindrical or tapered, 5–10 nerved, with a conspicuous white annulus at base, variously pubescent with short-bifid or trifid double hairs, glandular or glabrous; pappus of numerous white to tawny, barbellate to plumose capillary bristles; chromosome number $x = 19$.

Subgenus *Arctica* Maguire, Brittonia 406. 1943.

Stems simple or occasionally branched, arising from a short branched rhizome covered in imbricate scales and leaf-base remnants which may have tufts of long hairs in their axils (excessively developed in *A. fulgens*); cauline leaves narrow, 1.5–20 times as long as wide, occurring below the middle of the stem, linear to ovate, or oblanceolate to spathulate, elliptic or oblong, margins entire, denticulate to dentate or occasionally undulate, sessile to broadly or narrowly-winged petiolate, the petioles mostly shorter than the blade (except in *A. lonchophylla*), 1–5 (–7) pairs of leaves, the uppermost sessile and reduced; periclinium very conspicuous, scantily to densely lanate-pilose; capitula large, 1–5 (–8), radiate, broadly hemispheric to campanulate-turbinate; involucral bracts biseriate, lanceolate to oblanceolate; ray and disc florets yellow to orange; anthers yellow; pappus white, barbellate.

KEY TO THE SPECIES OF SUBGENUS *ARCTICA*

1. Achenes glabrous below and sparsely hirsute above or glabrous throughout; lower cauline leaves broad, 1.5–7 times as long as wide; capitula 1 (–3) 2
   2. Leaves conspicuously short stipitate-glandular; involucral bracts sparingly pilose otherwise glabrous, uniformly short stipitate-glandular; capitula nodding in anthesis; achenes glandular towards summit or occasionally densely glandular throughout ..... **1.** *A. louiseana*
   2. Leaves sparsely or not at all short stipitate-glandular; involucral bracts pilose at base becoming glabrous or remaining pilose above, rarely short stipitate-glandular; capitula erect or nodding in anthesis; achenes rarely glandular ..... **2.** *A. frigida*
1. Achenes densely hirsute throughout; lower cauline leaves narrow, 3–20 times as long as wide; capitula 1–5 (–8) 3

3. Lower cauline leaves sessile or petiole very short and broad-winged; ligules entire or minutely 3-toothed, if toothed the teeth less than 0.5 mm long; stems caespitose . . . . . **3.** *A. rydbergii*

3. Lower cauline leaves distinctly petiolate; ligules obviously 3-toothed, the teeth 0.1–7 mm long; stems solitary or few 4

4. Lower cauline leaves regularly denticulate or dentate; petiole narrow and approximately equalling the blade in length; capitula campanulate-turbinate . . . . . **4.** *A. lonchophylla*

4. Lower cauline leaves entire or irregularly denticulate or dentate; petiole narrow or broad-winged and shorter than the blade; capitula broadly hemispheric or hemispheric 5

5. Leaves linear to broadly lanceolate, acute or acuminate, entire, denticulate or dentate; florets yellow; capitula hemispheric . . . . . **5.** *A. angustifolia*

5. Leaves narrowly oblong to oblanceolate, obtuse, entire or remotely denticulate; florets dark orange-yellow; capitula broadly hemispheric 6

6. Base of stem with dense tufts of long brown woolly hair in axils of basal leaves and persistent leaf bases; disc corollas densely pilose . . . . . **6.** *A. fulgens*

6. Base of stem lacking axillary tufts of brown hair, occasionally with few whitish hairs; disc corollas not at all pubescent . . . . . **7.** *A. sororia*

TREATMENT OF INDIVIDUAL TAXA

1. **Arnica louiseana** Farr, Ottawa Nat. 20: 109. 1906. *A. louiseana* Farr subsp. *genuina* Maguire, Brittonia 4: 419. 1943. TYPE: "Lake Louise, Canadian Rocky Mts. Rockslide on Fairview Mt. Alt. about 6000 ft. Aug. 18, 1905. *E. M. Farr 1067.*" (HOLOTYPE: PH!; ISOTYPE: GH).

Plants 4–20 cm tall; rhizomes slender and covered with numerous dark imbricate scales and remnant leaf bases; stems solitary, simple, puberulent, stipitate-glandular, leaves to middle of stem or rarely all basal; leaves (0–) 1–3 pairs; upper cauline leaves sessile or narrowed to a short-winged petiole; lower cauline leaves 13–75 mm long, 4–20 mm wide; obtuse or occasionally acute or acuminate, elliptic to

oblong to ovate-lanceolate, petioles long and narrow, margins entire to saliently denticulate to slightly undulate, glabrous to hispidulous-puberulent, conspicuously short stipitate-glandular, 3–5 nerved; capitula nodding in anthesis, 1 (–3), campunulate-turbinate, 8–17 mm wide, 9–20 mm long; periclinium scantily to moderately pilose, yellow, short stipitate-glandular; involucral bracts 8–15, 8–12 mm long, 1.5–3 mm wide, narrowly lanceolate, acuminate, sparingly pilose otherwise glabrous, uniformly short stipitate-glandular; ligulate florets 7–10, yellow, 12–20 mm long, 2.5–4.6 mm wide, the teeth 0.2–1.5 mm long; disc florets 6.2–8.4 mm long, narrowly goblet-shaped, stipitate-glandular, pilose, the tube 2–3.1 mm long; achenes 3.2–5 mm long, glabrous below and sparsely hirsute above or glabrous throughout, glandular towards summit or occasionally densely glandular throughout; chromosome number $2n = 76, 95$.

DISTRIBUTION AND HABITAT. Infrequent and localized on exposed tundra slopes and mature calcareous rock slides at 1800–2100 meters in the Canadian Rocky Mountains primarily in the vicinities of Waterton, Jasper and Banff National Parks (Figure 1). Flowers July to August.

Arnica louiseana can be separated from all other arnicas by its evident glandularity, its small size, and the nodding tendency of its peduncle.

2. **Arnica frigida** Meyer ex Iljin, Trav. Musc. Bot. Acad. Sci. URSS. 19: 112. 1926.

Plants 0.5–4 dm tall; rhizomes short, slender, branched and covered with numerous dark imbricate scales and remnant leaf bases; stems solitary or several, rarely branching, glabrous to hispidulous-puberulent and sparsely stipitate-glandular below becoming sparsely to densely hispidulous-pilose and more glandular near the periclinium; leaves of small plants crowded at base, 1–4 pairs; upper cauline leaves sessile or narrowed to a short-winged petiole; lower cauline leaves 12–100 mm long, 5 35 mm wide, acute or obtuse, elliptic to lanceolate or ovate, or oblanceolate to spathulate, or occasionally lanceolate-oblong, acute to obtuse or abruptly pointed, petioles narrow and as long as the blade, margins inconspicuously denticulate or dentate to slightly undulate, rarely entire, glabrous to sparingly hispidulous-puberulent and sparsely or not at all short stipitate-glandular, 3–5 nerved; capitula erect or nodding in anthesis, 1 (–3), hemispheric to occasionally campanulate-turbinate, 8–20 mm wide, 11–30 mm long; periclinium sparsely to densely

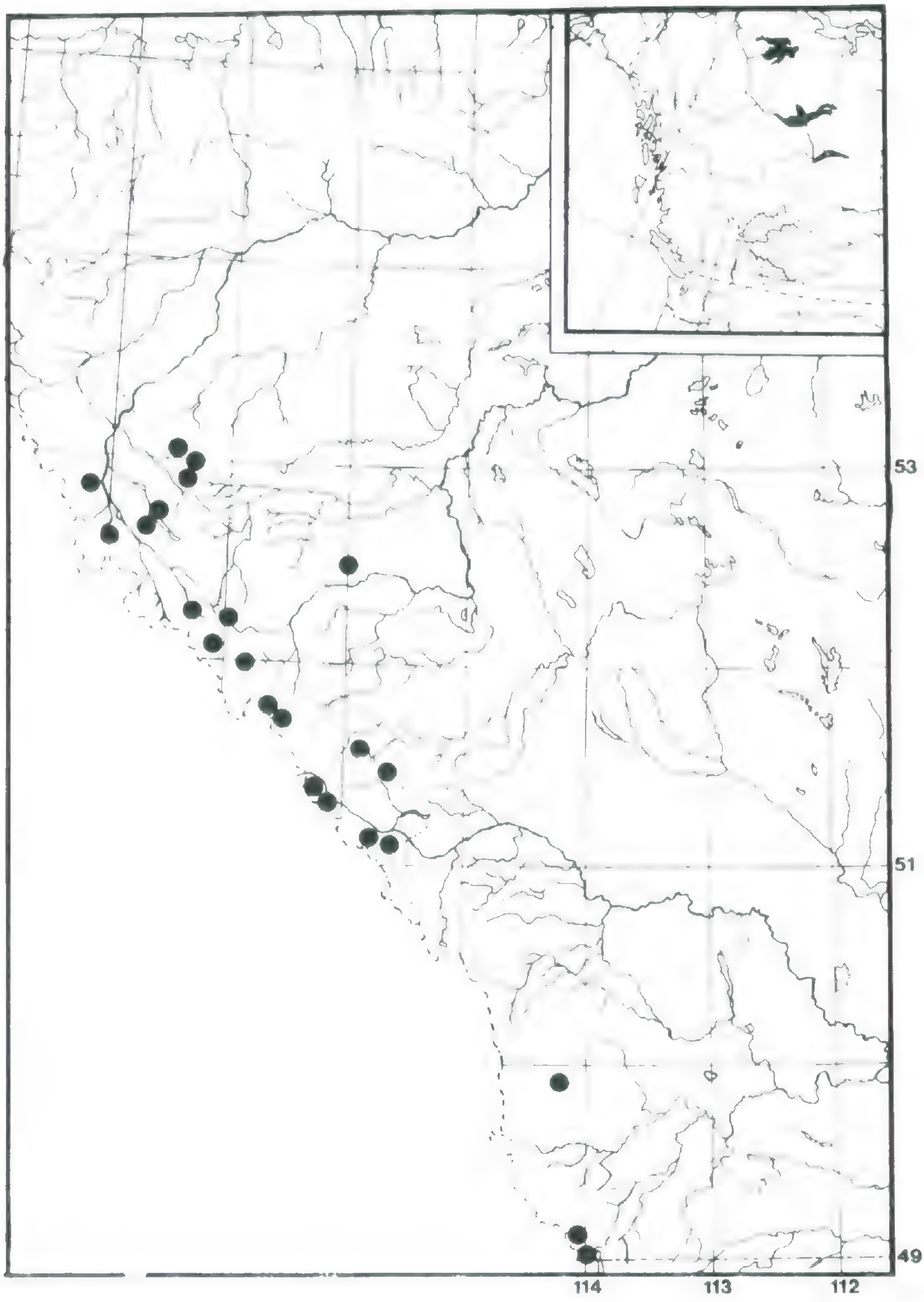


Figure 1. Distribution of *Arnica louiseana* in southwestern Alberta. Shaded area of inset corresponds to area covered by distribution map.

lanate-pilose, white or yellow, rarely stipitate-glandular; involucral bracts 9–20, 7.5–14.5 mm long, 1.8–4.9 mm wide, lanceolate to oblanceolate, acute, acuminate or rarely obtuse, pilose at base becoming glabrous or remaining pilose above, rarely short stipitate-glandular; ligulate florets 6–17, yellow, 10–39 mm long, 2.3–8 mm wide, the teeth 0.4–5 mm long; disc florets 6–10.2 mm long, goblet-shaped, sparingly stipitate-glandular, pilose, the tube 2–3.9 mm long; achenes 2.5–6 mm long, glabrous below and sparsely hirsute above or glabrous throughout, rarely glandular; chromosome number $2n = 38, 57, 76, 95$.

Arnica frigida is extremely variable in pubescence and leaf form. These plants are, however, characterized by their acute to obtuse or abruptly pointed apices; elliptic, lanceolate or spathulate leaves; achenes that are glabrous at the base and sparsely hirsute at the summit; and often with only a single capitulum. The two subspecies in *A. frigida* can be separated by the suite of characters in the key below. A discussion of the taxonomic history and synonymy of *A. frigida* is presented in Downie and Denford (1986a).

KEY TO THE SUBSPECIES OF *ARNICA FRIGIDA*

1. Periclinium yellow; involucral bracts pilose at base becoming glabrous or remaining pilose above, 1.8–4.9 mm wide; plants 0.6–4 dm tall ..... **2a.** subsp. *frigida*
1. Periclinium white; involucral bracts pilose at base becoming glabrous above, 2.5–4.6 mm wide; plants 0.5–2.5 dm tall ..... **2b.** subsp. *griscomii*

2a. **Arnica frigida** Meyer ex Iljin subsp. **frigida,** Trav. Musc. Bot. Acad. Sci. URSS. 19: 112. 1926. *A. louiseana* Farr subsp. *frigida* (Meyer ex Iljin) Maguire, Madroño 6: 153. 1942. *A. louiseana* Farr var. *genuina* Maguire, Madroño 6: 153. 1942. *A. louiseana* Farr var. *frigida* (Meyer ex Iljin) Welsh, Great Basin Nat. 28: 149. 1968. TYPE: "St. Laurence Bay (and Eschscholtz Bay), 1815–1818. *Eschscholtz s.n.*" (HOLOTYPE: LE, photo CAN!, UC!; ISOTYPE: LE, photo UC!)

A. nutans Rydb., N. Amer. Fl. 34: 328. 1927. TYPE: "Alaska, Vicinity of Port Clarence. Hillsides along Tuksuk Channel, near Port Clarence. July 30, 1901. *F. A. Walpole 1618.*" (HOLOTYPE: NY!, photo CAN!, UC!; ISOTYPE: US, photo UC!).

A. sancti-laurentii Rydb., N. Amer. fl. 34: 328. 1927. TYPE: "Sinu St. Laurentii. *Chamisso s.n.*" (HOLOTYPE: GH, photo CAN!, UC!).

A. brevifolia Rydb., N. Amer. Fl. 34: 329. 1927. *A. louiseana* Farr var. *brevifolia* (Rydb.) Maguire, Madroño 6: 153. 1942. TYPE: "Alaska, Copper River Region.

Near Camp 6/15–19, in lateral moraine of Chitaslene Glacier. June 19, 1902. *W. L. Poto 46.*" (HOLOTYPE: US!, photo CAN!, UC!, drawing NY!).

A. mendenhallii Rydb., N. Amer. Fl. 34: 329. 1927. *A. louiseana* Farr var. *mendenhallii* (Rydb.) Maguire, Madroño 6: 153. 1942. TYPE: "Alaska. Fort Hamlin, Yukon River to Bergman, Koyukuk River. Found on Old Man Creek, a branch of the Koyukuk River. July 8, 1901. *W. C. Mendenhall s.n.*" (HOLOTYPE: US!, photo CAN!, UC!, drawing NY!).

A. illiamnae Rydb., N. Amer. Fl. 34: 331. 1927. *A. louiseana* Farr var. *illiamnae* (Rydb.) Maguire, Madroño 6: 15. 1942. TYPE: "Alaska. Lake Iliamna region. Open tundra along Nogheling Trail. July 20, 1902. *M. W. Gorman 163.*" (HOLOTYPE: US!, photo CAN!, UC!).

A. louiseana Farr var. *pilosa* Maguire, Madroño 6: 154. 1942. TYPE: "Alaska. Igloo Creek, McKinley National Park. July 13, 1932. *J. Dixon 29.*" (HOLOTYPE: UC!; ISOTYPE: US).

A. snyderi Raup, Sargentia 6: 250. 1947. TYPE: "Alpine crevices and slide rock. Vicinity of Brintnell Lake. App. Lat. 62° 5′ N., Long. 127° 325′ W, north slope of Colonel Mt., S. W. Mackenzie. July 5, 1939. *H. M. Raup & J. H. Soper 9383.*" (HOLOTYPE: RM!; ISOTYPE: CAN!).

A. frigida var. *glandulosa* Boivin, Rhodora 55: 56. 1953. TYPE: "Yukon Territory, Canada. Steep rocky slope by Klondike River. About 20 miles east of Dawson on road to McQuesten. July 17, 1949. *J. A. Calder & L. G. Billard 3767.*" (HOLOTYPE: DAO!).

Plants 0.6–4 dm tall; leaves 2–4 pairs; lower cauline leaves 12–100 mm long, 5–35 mm wide, acute or obtuse or abruptly pointed, lanceolate, elliptic to elliptic-lanceolate, spathulate or rarely oblanceolate; capitula 1 (3), 8 20 mm wide, 11 30 mm long; periclinium sparsely to densely lanate-pilose, yellow; involucral bracts 7.5–14.5 mm long, 1.8–4.9 mm wide, lanceolate, acuminate or rarely obtuse, pilose at base becoming glabrous or remaining pilose above; ligulate florets 7–17, 10–39 mm long, 2.3–8 mm wide, the teeth 1–5 mm long; achenes 3.2 6 mm long; chromosome number $2n = 38, 57, 76, 95$.

DISTRIBUTION AND HABITAT. Abundant in alpine meadows, tundras and calcareous rocky outcrops from the Kolyma River, U.S.S.R., east to the islands of Bering Strait, Alaska, Yukon Territory to the Mackenzie River, Northwest Territories (Figure 2). Scattered populations found north of the Arctic Circle and east to the Coppermine River in Northwest Territories, and infrequent to rare in alpine areas of northern British Columbia. Flowers June to July.

2b. **Arnica frigida** Meyer ex Iljin subsp. **griscomii** (Fern.) S. R. Downie, Canad. J. Bot. 64: 1369. 1986. *A. griscomii* Fern., Rhodora 26: 105. 1924. *A. louiseana* Farr subsp. *griscomii* (Fern.) Maguire, Brittonia 4: 419. 1943. *A. louiseana* Farr var.

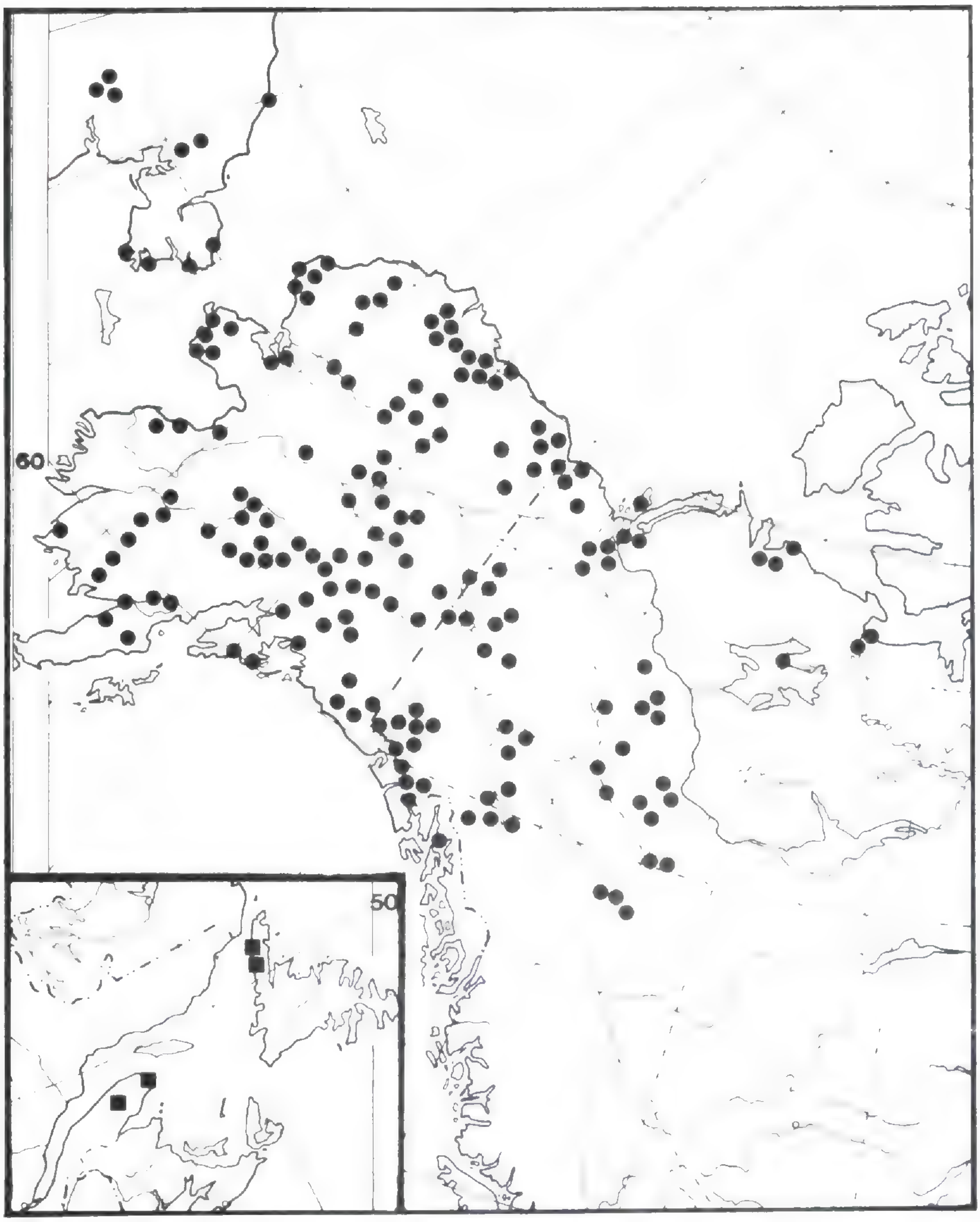


Figure 2. Distribution of *Arnica frigida* subsp. *frigida* (●) and *A. frigida* subsp. *griscomii* (■).

griscomii (Fern.) Boivin, Phytologia 23: 95. 1972. TYPE: "Québec. Matane County. Cold chimneys in the schist at about 900–1000 m altitude, south of Fernald Pass, Mt. Mattaouisse. Aug. 20, 1923. *M. L. Fernald & L. B. Smith 26084.*" (HOLOTYPE: GH!, photo CAN!, ISOTYPES: CAN!; MT!, UC!, photo UC!).

Plants 0.5–2.5 dm tall; leaves 1–2 pairs; lower cauline leaves 15–80 mm long, 6–25 mm wide, acute or obtuse, spathulate to ovate or lanceolate-oblong; capitula 1 (–3), 11–20 mm wide, 12–23 mm long; periclinium moderately pilose, white; involucral bracts 9–13.5 mm long, 2.5–4.6 mm wide, broadly lanceolate to oblanceolate, acuminate or obtuse, pilose at base becoming glabrous above; ligulate florets 6–11, 15–22 mm long, 3–6 mm wide, the teeth 0.4–1.8 mm long; achenes 2.5–4.5 mm long; chromosome number $2n = 76$.

DISTRIBUTION AND HABITAT. Rare on exposed hornblende-schists and dry schistose talus in the alpine areas (850–1070 meters) of Mts. Logan and Saint-Alban of the Gaspé Peninsula in Québec; and infrequent in the turfy talus of limestone sea-cliffs and gravelly limestone barrens in the areas of Ingornachoix Bay, St. John Bay, St. Barbe Bay and the Doctor Hill Range of northwestern Newfoundland (Figure 2). Flowers June to July.

3. **Arnica rydbergii** Greene, Pittonia 4: 37. 1899. TYPE: "Flora of Central Montana. Little Belt Mts., near the Pass. Aug. 10, 1896. *J. H. Flodman 891.*" (HOLOTYPE: ND!, ISOTYPES: NY!, US!, photo CAN!).

A. caespitosa A. Nels., Bot. Gaz. 30: 203. 1900. TYPE: "Yellowstone National Park, on high stony ridges, Druid Peak, Wyoming. July 12, 1899. *A. & E. Nelson 5785.*" (HOLOTYPE: RM!; ISOTYPES: RM!).

A. tenuis Rydb., Bull. Torrey Bot. Club 28: 20. 1901. TYPE: "Big Horn Mountains, Sheridan Co., Northwestern Wyoming. Aug. 1899. *F. Tweedy 2094.*" (HOLOTYPE: NY, photo CAN!).

A. aurantiaca Greene, Torreya 1: 42. 1901. TYPE: "Eastern Oregon Plants. Head of Keystone Creek, Wallowa Mtns. Aug. 2, 1900. *Wm. C. Cusick 2451.*" (ISOTYPE: RM!, US).

A. lasiosperma Greene, Leaflets 2: 48. 1910. TYPE: Estes Park, base of Long's Peak, Colorado. 26 Aug. 1895. *Osterhout s.n. fide* Maguire (1943). Type not seen.

A. cascadensis St. John, Rep. Prov. Mus. Nat. Hist. B.C. 1926: 10. 1927. TYPE: "Mt. McLean, British Columbia. July 11, 1926. *W. B. Anderson 8003.*" (HOLOTYPE: WS, photo CAN!).

A. sulcata Rydb., N. Amer. Fl. 34: 344. 1927. TYPE: "Scott Mountain, Siskiyou County, California. Aug. 22, 1896. *E. L. Greene 1005.*" (HOLOTYPE: GH, drawing NY!).

A. ovalis Rydb., N. Amer. Fl. 34: 338. 1927. TYPE: "Crow Nest Pass, Rocky Mtns. July 31, 1897. *J. M. Macoun 72719.*" (HOLOTYPE: CAN!, photo CAN!).

Plants 0.8–3.5 dm tall; rhizomes moderately long and densely covered with scales and leaf base remnants; stems caespitose, several branches arising from the rhizome tip, simple, sparsely puberulent becoming moderately pubescent upwards, stipitate-glandular; leaves 2–4 pairs; upper cauline leaves sessile, lanceolate to broadly lanceo-

late; lower cauline leaves 2–7 cm long, 0.5–2.5 cm wide, acute to occasionally obtuse, oblanceolate to spathulate, sessile or petioles very short and broad-winged, margins entire to occasionally denticulate to sometimes predominantly dentate, glabrous to sparsely pilose, stipitate-glandular, 3–5 nerved; capitula erect, 1–3 (–5), campanulate-turbinate, 9–15 mm wide, 7 22 mm long; periclinium moderately pilose, white, short stipitate-glandular; involucral bracts 9–15, 7.3–14.5 mm long, 1.3 3.1 mm wide, linear-oblong to narrowly lanceolate, acute, glabrous to sparingly pilose, stipitate-glandular; ligulate florets 6–10, yellow, 13.5–29 mm long, 4–8.5 mm wide, entire or minutely 3-toothed, if toothed the teeth 0.1–0.5 mm long; disc florets 6.1–9.1 mm long, narrowly tubular, stipitate-glandular, densely pilose, the tube 2.3 3.7 mm long; achenes 3.8–7.1 mm long, densely hirsute throughout, not stipitate-glandular; chromosome number $2n = 38, 76$.

DISTRIBUTION AND HABITAT. Dry to mesic, exposed, rocky alpine slopes and ridges or alpine meadows in the Rocky Mountains of Alberta and British Columbia, south in the Cascade Mountains to Washington and Oregon, the Uinta Mountains of Utah and the Rocky Mountains of Wyoming and Colorado (Figure 3). Also known from Vancouver Island. Flowers July to August.

Confined to the cordillera of western North America, *Arnica rydbergii* is readily distinguished by its small, narrow heads; its minutely denticulate or entire ligule margins; few and narrowly tubular disc florets; clustered stems; and a strong tendency for the lower cauline leaves to be sessile.

During the period 1899 to 1901, four names were proposed for this species, including *Arnica rydbergii* Greene. As previously suggested by Maguire (1943), and observed in this study, the type specimens of *A. caespitosa, A. tenuis* and *A. aurantiaca* all fall within acceptable species limits and were undoubtedly named before the application of *A. rydbergii* was fully understood. The type of *A. cascadensis,* although not seen in this study, was described as a glandless *A. rydbergii,* for it maintains all other diagnostic features (Maguire, 1943). The presence (or absence) of short stipitate-glandular hairs on the leaves and periclinium is not a critical character. *Arnica lasiosperma* is merely a depauperate specimen of *A. rydbergii* (Maguire, 1943).

The short-petiolate and large oval basal leaves led Rydberg to propose *Arnica ovalis* as a new species in 1927. However, its entire to indistinctly denticulate ligules, the narrow capitulum, and the sessile cauline leaves strongly suggest that this species conforms to

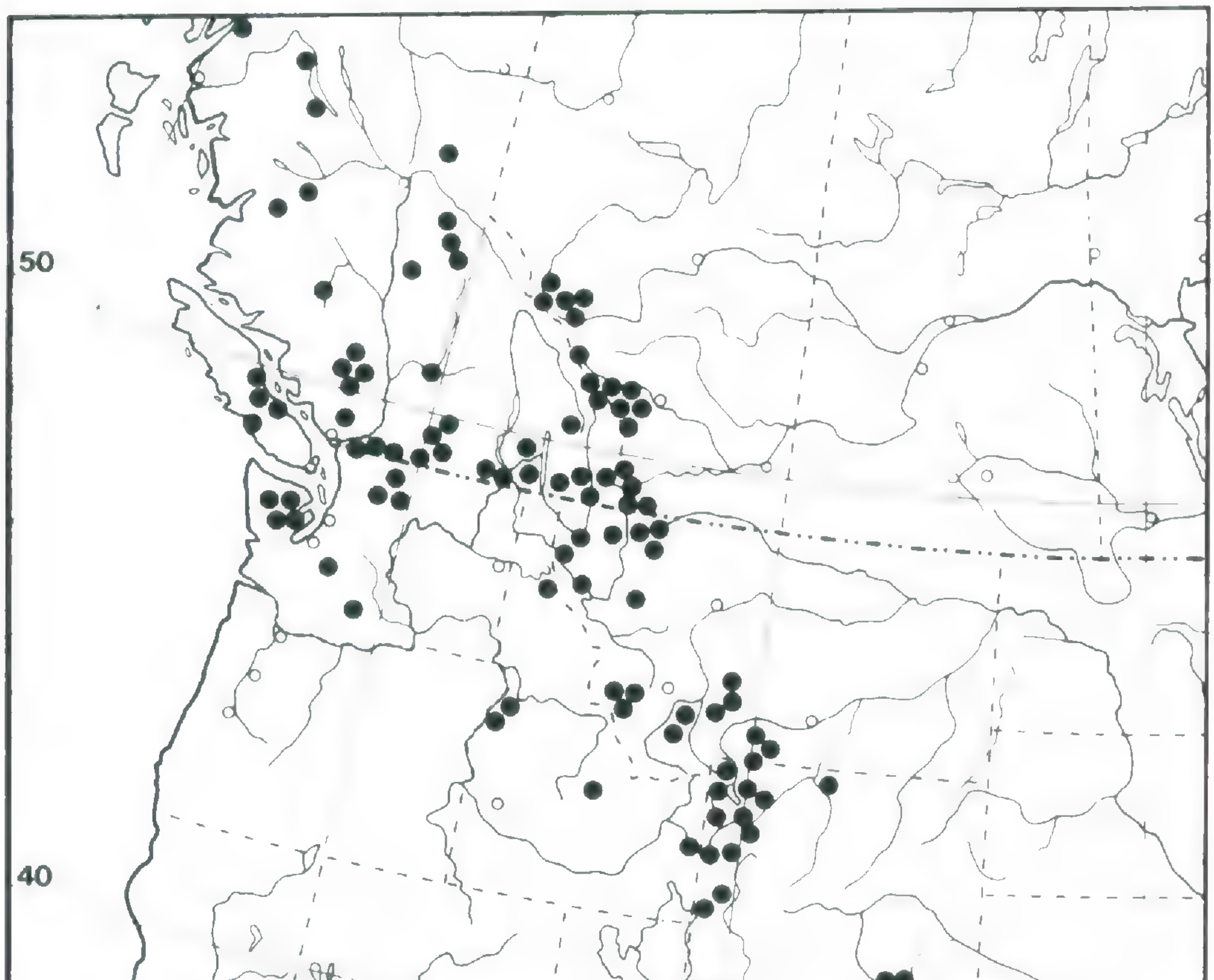


Figure 3. Distribution of *Arnica rydbergii.*

A. rydbergii. In the same year, Rydberg proposed *A. sulcata* for a single specimen possessing a short-plumose pappus, and a sulcate and copiously glandular stem. Maguire (1943) observed similarities between this and *A. rydbergii,* and placed *A. sulcata* in synonymy with the latter. With the presence of this plumose pappus it is doubtful if this species belongs in *A. rydbergii.* In addition, the range of *A.*

rydbergii does not extend south to California. However, without observing this specimen, it is difficult to assign it to a particular taxon. Until subsequent collections and observation reveal this taxon to be distinct, it should remain in synonymy with *A. rydbergii.*

4. **Arnica lonchophylla,** Pittonia 4: 164. 1900.

Plants 1.2–5 dm tall; rhizomes slender, branched, covered with numerous dark imbricate scales and remnant leaf bases; stems solitary or few, simple or branched, glabrous to sparsely puberulent and moderately stipitate-glandular becoming densely pubescent and glandular upwards; leaves 3–7 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 3.5–14 cm long, 0.5–3.7 cm wide, acute, narrowly to broadly lanceolate to ovate, distinctly petiolate, petioles narrow and approximately equalling the blade in length, margins regularly dentate or denticulate, glabrous to moderately pilose, sparsely to densely stipitate-glandular, 3–7 nerved; capitula erect, (1–) 3–7 (–8), campanulate-turbinate, 7 20 mm wide, 8 16 mm long; periclinium glabrous to moderately pilose, white, stipitate-glandular; involucral bracts 10–15, 6.1–11.5 mm long, 1.2–3.5 mm wide, narrowly lanceolate, acute, glabrous to moderately pilose, stipitate-glandular; ligulate florets 6–14, yellow, 10–26 mm long, 3–7.1 mm wide, 3-toothed, the teeth 0.1–2.1 mm long; disc florets 5–9.5 mm long, narrowly goblet-shaped or goblet-shaped, moderately to densely pilose with long or short hairs, sparsely to densely stipitate-glandular, the tube 1.9–4 mm long; achenes 3–5.9 mm long, densely hirsute throughout, occasionally to regularly stipitate-glandular; chromosome number $2n = 38, 57, 76$.

In his monographic treatment of the genus, Maguire (1943) recognized three subspecies within *Arnica lonchophylla: genuina, chionopappa* and *arnoglossa.* The subspecific epithet *genuina* is illegitimate and should be treated as *lonchophylla.* Ediger and Barkley (1978), however, did not recognize infraspecific taxa within *A. lonchophylla* and maintained that the small differences among them do not warrant taxonomic recognition. Material from eastern Canada, previously recognized as subsp. *chionopappa,* is inseparable from widespread northwestern Canadian populations. Two subspecies are recognized within *A. lonchophylla: lonchophylla* and *arnoglossa.* The morphological characters delimiting these taxa are described below.

KEY TO SUBSPECIES OF *ARNICA LONCHOPHYLLA*

1. Periclinium and involucral bracts moderately pilose; disc corolla goblet-shaped, sparsely stipitate-glandular, densely long pilose; leaves sparsely stipitate-glandular, glabrous to moderately pilose, 3 11 times as long as wide .... **4a.** subsp. *lonchophylla*

1. Periclinium and involucral bracts glabrous to sparsely puberulent; disc corolla narrowly goblet-shaped, densely stipitate-glandular, moderately short pilose; leaves densely stipitate-glandular, glabrous to sparsely puberulent, 3 5 times as long as wide.... ..... **4b.** subsp. *arnoglossa*

4a. **Arnica lonchophylla** Greene subsp. **lonchophylla,** Pittonia 4: 164. 1900. *A. lonchophylla* Greene subsp. *genuina* Maguire, Brittonia 4: 430. 1943. *A. alpina* (L.) Olin var. *lonchophylla* (Greene) Welsh, Great Basin Nat. 28: 149. 1968. *A. alpina* (L.) Olin subsp. *lonchophylla* (Greene) G. W. Douglas & G. Ruyle-Douglas in Taylor and MacBryde, Canad. J. Bot. 56: 185. 1978. *A. angustifolia* Vahl subsp. *lonchophylla* (Greene) G. W. Douglas & G. Ruyle-Douglas, Canad. J. Bot. 56: 1710. 1978. TYPE: "Athabasca River, Lat. 53° 30′, Alberta. June 25, 1898. *W. Spreadborough 19647.*" (HOLOTYPE: ND!; ISOTYPE: CAN!, photo CAN!).

A. wilsonii Rydb., N. Amer. Fl. 34: 332. 1927. TYPE: "W. of James Bay, 140 miles up Kapiscow River, Ont. July 15, 1902. *W. J. Wilson 54043.*" (HOLOTYPE: CAN!).

Arnica chionopappa Fern., Rhodora 7: 148. 1905. *A. lonchophylla* Greene subsp. *chionopappa* (Fern.) Maguire, Brittonia 4: 430. 1943. TYPE: "Wet cliffs, Banks of the Grand River, Gaspé County, Québec. June 30 July 3, 1904. *M. L. Fernald s.n.*" (HOLOTYPE: GH!, photo CAN!).

A. gaspensis Fern., Rhodora 7: 148. 1905. TYPE: "Dry precipitous ledges of a hill at Cap Tourelle near St. Anne des Monts, Gaspé Co., Lower Canada. July 16, 1881. *J. A. Allen s.n.*" (HOLOTYPE: GH!, photo CAN!).

A. fernaldii Rydb., N. Amer. Fl. 34: 333. 1927. TYPE: "Newfoundland, Region of Port au Port Bay, Dry exposed ledges and shingle on the limestone tableland, Table Mountain, July 16 and 17, 1914. *M. L. Fernald & H. St. John 10875.*" (HOLOTYPE: NY; ISOTYPES: CAN!, GH!, RM!).

Plants 1.2–5 dm tall; leaves 3–7 pairs; lower cauline leaves 3.5–14 cm long, 0.5–3.7 cm wide, narrowly lanceolate to ovate, margins regularly denticulate or dentate, glabrous to moderately pilose, sparsely stipitate-glandular, 3 5 nerved; capitula (1–) 3 5 (–8), 7–20 mm wide, 8–16 mm long; periclinium moderately pilose, white, stipitate-glandular; involucral bracts 7–11.5 mm long, 1.3–3.5 mm wide, moderately pilose throughout, stipitate-glandular; ligulate

florets 6–14, 13–26 mm long, 3–7.1 mm wide, the teeth 0.1–2.1 mm long; disc florets 5.1–9.5 mm long, goblet-shaped, densely long pilose, sparsely stipitate-glandular, the tube 1.9–4 mm long; achenes 3–5.9 mm long, occasionally short stipitate-glandular; chromosome number $2n = 57, 76$.

DISTRIBUTION AND HABITAT. Dry to mesic, open montane slopes of the Canadian Rockies extending northward in the interior lowlands to the Arctic Circle. Its range extends from the Yukon Territory, eastward through southwestern Northwest Territories, the northern regions of Saskatchewan and Manitoba to Hudson Bay with disjunct populations in northeastern Minnesota and adjacent Ontario, the Gaspé Peninsula, Anticosti Island, New Brunswick, Nova Scotia, and western Newfoundland (Figure 4). In eastern Canada, plants are found in open woodlands, river gravels, shorelines, and calcareous rocky outcrops, precipices and barrens. Flowers June to August.

In the past, *Arnica lonchophylla* subsp. *lonchophylla* from south central Ontario has either been regarded as a separate species (i.e., *A. wilsonii;* Rydberg, 1927), or a hybrid between *A. angustifolia* and *A. lonchophylla* (Maguire, 1943). Subsequent collections led Ediger and Barkley (1978) to place the name *A. wilsonii* in synonymy with *A. lonchophylla.* All material seen by the authors falls within the normal range of variation of typical *A. lonchophylla* subsp. *lonchophylla.*

In 1927, Rydberg reduced *Arnica chionopappa* to *A. arnoglossa,* and described the Newfoundland *A. chionopappa* as *A. fernaldii.* Fernald (1933) was unable to detect any differences between *A. chionopappa* from Gaspé, Anticosti Island, New Brunswick and Newfoundland, and inferentially reduced *A. fernaldii* to *A. chionopappa.* Maguire (1943) noticed that plants from Newfoundland are usually somewhat smaller and have narrower leaves than those from Québec. The greater number of herbarium specimens examined during this study showed no statistically significant differences between Newfoundland and Québec material.

Arnica gaspensis was proposed by Fernald in 1905 for plants similar to *A. chionopappa* but having larger, less hirsute achenes, oblanceolate bracts, more sharply toothed ligules, and a creamy-white pappus. These plants are similar to *A. lonchophylla* subsp. *lonchophylla.*

In northwestern Canada, where the ranges of *Arnica angustifolia* subsp. *angustifolia* and *A. lonchophylla* overlap, some specimens

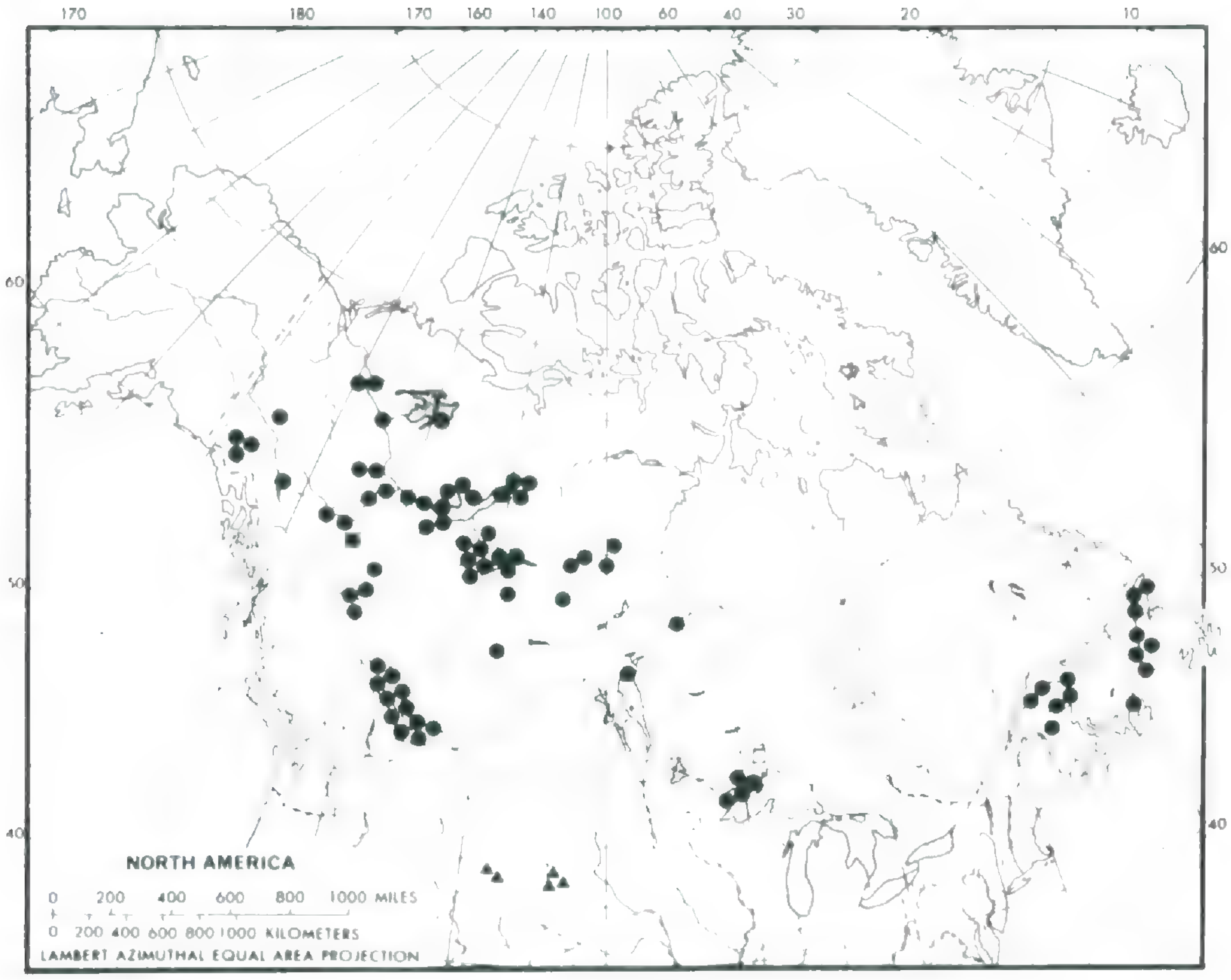


Figure 4. Distribution of *Arnica lonchophylla* subsp. *lonchophylla* (●) and *A. lonchophylla* subsp. *arnoglossa* (Δ).

cannot be assigned to either taxon without difficulty. This similarity in morphology led Douglas and Ruyle-Douglas (1978) to propose *A. angustifolia* subsp. *lonchophylla*. The status of these two taxa is further confounded by their flavonoid chemistry, for no differences are apparent. In addition, both share the same ploidy levels. Where the ranges do not overlap, *A. lonchophylla* and *A. angustifolia* are separated with ease. *Arnica lonchophylla* subsp. *arnoglossa* and the eastern Canadian disjunct of *A. lonchophylla* subsp. *lonchophylla* are evidently long-petiolate, have prominent regularly dentate teeth and obvious campanulate-turbinate capitula. Similarly, *A. angustifolia* from Scandinavia, the U.S.S.R., Greenland and eastern Canada show a great degree of morphological uniformity. *Arnica lonchophylla* is also typically a plant of montane or lowland habitats, whereas *A. angustifolia* is arctic and alpine. Nevertheless, in northwestern Canada, evidence suggests that these two taxa may be hybridizing; however, the actual extent of hybridization is unknown.

4b. **Arnica lonchophylla** subsp. **arnoglossa** (Greene) Maguire, Brittonia 4: 431. 1943. *A. arnoglossa* Greene, Pittonia 4: 166. 1900. *A. lonchophylla* Greene var. *arnoglossa* (Greene) Boivin, Nat. Can. 87: 27. 1960. TYPE: "Black Hills, near Fort Meade, S. Dakota. June 11, 1887. *W. H. Forwood 323 1/2.*" (HOLOTYPE: US!, photo CAN!).

A. arcana A. Nels., Bot. Gaz. 37: 276. 1904. TYPE: Doyle Creek, Big Horn Mtns., Wyoming. July 26, 1902. *Goodding 377 fide* Ediger and Barkley (1978). Type not seen.

A. rydbergii var. *dubia* A. Nels. ex Hayward, Bot. Gaz. 85: 384. 1928, *Nomen nudum.*

Plants 1.7–4.5 dm tall; leaves 3–5 pairs; lower cauline leaves 4.5 11 cm long, 1.2–3 cm wide, broadly lanceolate to ovate, margins regularly denticulate to occasionally dentate, glabrous to sparsely puberulent, densely stipitate-glandular, 5–7 nerved; capitula (1–) 3–7 (–8), 7–13 mm wide, 9–13 mm long; periclinium glabrous to sparsely puberulent, white, densely stipitate-glandular; involucral bracts 6.1–10 mm long, 1.2–2.4 mm wide, glabrous to sparsely puberulent, densely stipitate-glandular; ligulate florets 7–10, 10–17.5 mm long, 3–5 mm wide, the teeth 0.2 1.1 mm long; disc florets 5–8.5 mm long, narrowly goblet-shaped, moderately short pilose, densely stipitate-glandular, the tube 2 3.2 mm long; achenes 3–5 mm long, regularly short stipitate-glandular; chromosome number $2n = 38$.

DISTRIBUTION AND HABITAT. Extremely localized in the Big Horn Mountains of north central Wyoming and the Black Hills region of South Dakota (Figure 4). Apparently quite rare. Plants of moist rocky soils and open woodlands. Flowers July to August.

Arnica lonchophylla subsp. *arnoglossa* is restricted to the Black Hills of South Dakota and the Big Horn mountains of Wyoming. It is readily distinguished from *A. lonchophylla* subsp. *lonchophylla* by its broader leaves, narrower disc corollas, and glandular but sparsely puberulent leaves, disc corollas, periclinium and involucral bracts.

5. **Arnica angustifolia** Vahl in Hornem., Fl. Dan. 9(26): 5. 1816.

Plants 0.5–5.4 dm tall; rhizomes slender, branched and covered in imbricate scales and leaf base remnants that may have tufts of long hairs in their axils; stems solitary or few, simple or rarely branched, sparsely to densely villous, short stipitate-glandular becoming incresingly villous and glandular upwards; leaves 1–5 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 2–20 cm

long, 0.3–4.1 cm wide, acute or acuminate, linear to broadly lanceolate, petioles short and broad-winged or narrow-winged and shorter than the blade, margins entire to irregularly denticulate or dentate, glabrous to densely spreading woolly-villous, stipitate-glandular, 3-5 nerved; capitula erect, 1-3 (–5), hemispheric, 12–30 mm wide, 9–21 mm long; periclinium very conspicuous, moderately to densely pilose, white, stipitate-glands occasionally lacking, obscured or dense; involucral bracts 9–22, 6.5 17.6 mm long, 1.5 4.1 mm wide, narrowly to broadly lanceolate to occasionally oblanceolate, acute or acuminate, densely to sparsely pilose throughout or evidently pilose at base becoming less so upwards, inconspicuously to obviously stipitate-glandular; ligulate florets 6–16, yellow, 10–40 mm long, 3–9.5 mm wide, 3-toothed, the teeth 0.2 7 mm long; disc florets 5 10 mm long, goblet-shaped, moderately to densely pilose, inconspicuously glandular or absent, the tube 1.9 4.1 mm long; achenes 3.1–7.6 mm long, densely hirsute throughout, inconspicuous or not at all glandular; chromosome number $2n = 38, 57, 76, 95$.

Arnica angustiolia, a circumpolar and circumboreal species, is the most widespread and most polymorphic in the genus. This taxon is identified by its long, linear to broadly lanceolate leaves, densely hirsute achenes, erect capitula, and yellow florets. Maguire (1943) segregated this species into seven geographical races; however, results of this investigation indicate that this aggregate is best treated as two distinct taxa: *A. angustifolia* subsp. *angustiifolia* (a combination of the previously recognized subspecies *angustifolia, attenuata, sornborgeri, intermedia, iljinii* and *alpina* of *A. angustifolia* and *A. plantaginea*) and *A. angustifolia* subsp. *tomentosa. Arnica angustifolia* subsp. *tomentosa* is a relatively small plant possessing one to three capitula and densely villous leaves, stems and involucral bracts. The periclinium is densely woolly-villous and conspicuously stipitate-glandular. *Arnica angustifolia* subsp. *angustifolia* is usually a much taller plant bearing one to five capitula per stem. Its leaves, stems and bracts are never densely villous. In many instances, the leaves are glabrous. The periclinium is usually pilose, but never woolly-villous, and stipitate-glands may be inconspicuous or lacking. A discussion of the taxonomic history and synonymy of *A. angustifolia* is presented in Downie (1988).

KEY TO SUBPSPECIES OF *ARNICA ANGUSTIFOLIA*

1. Leaves glabrous to moderately villous, entire to denticulate or rarely dentate, linear to broadly lanceolate; periclinium mod-

erately to densely pilose, stipitate-glands occasionally lacking or obscured ..... **5a.** subsp. *angustifolia*

1. Leaves densely spreading woolly-villous, entire or rarely denticulate, narrowly lanceolate; periclinium densely woolly-villous and densely stipitate-glandular ..... **5b.** subsp. *tomentosa*

5a. **Arnica angustifolia** Vahl in Hornem. subsp. *angustifolia*, Fl. Dan. 9(26): 5. 1816. *A. alpina* (L.) Olin var. *angustifolia* (Vahl) Fern., Rhodora 36: 96. 1934. *A. alpina* (L.) Olin subsp. *angustifolia* (Vahl) Maguire, Madroño 6: 153. 1942. TYPE: "E. Groenlancia. *Geiseke s.n.*." (HOLOTYPE: S!; ISOTYPE: C!).

A. alpina (L.) Olin forma *inundata* Porsild, Medd. Groenl. 58: 181. 1926. TYPE: Sargag, Greenland. *Porsild 200 fide* Maguire (1943). Type not seen.

A. alpina (L.) Olin var. *vahliana* Boivin, Nat. Can. 75: 209. 1948. TYPE: "Baffin Island. 1937. *V. C. Wynne-Edwards 7364" fide* Ediger and Barkley (1978). Type not seen.

Arnica montana L. var. *alpina* L., Sp. Pl. 884. 1753. *A. alpina* (L.) Olin, Dissert. de *Arnica*, Upsaliae 11. 1799. *A. alpina* (L.) Olin subsp. *genuina* Maguire, Brittonia 4: 408. 1943. *A. angustifolia* Vahl subsp. *alpina* (L.) I. K. Ferguson in Heywood, Bot. J. Linn. Soc. 67: 282. 1973. TYPE: "Habitat in Alpibus and pratis Europae frigidioris," as described in Linnaeus' *Species Plantarum* (1753) *fide* Maguire (1943). Type not seen.

Arnica attenuata Greene, Pittonia 4: 170. 1900. *A. alpina* (L.) Olin subsp. *attenuata* (Greene) Maguire, Madroño 6: 153. 1942. *A. alpina* (L.) Olin var. *attenuata* (Greene) Ediger & Barkl., N. Amer. Fl. 10: 31. 1978. *A. angustifolia* Vahl subsp. *attenuata* (Greene) G. W. Douglas & G. Ruyle-Douglas, Canad. J. Bot. 56: 1710. 1978. TYPE: "Open woods and river banks. Lewis River, Yukon Territory. June 13, 1899. *M. W. Gorman 1025.*" (ISOTYPE: CAN!, US!, photo CAN!).

A. lowii Holm, Repert. Spec. Nov. Regni. Veg. 3: 388. 1907. TYPE: "Severn River (Keewatin) Ont. August 5, 1886. *J. Macoun 14699.*" (HOLOTYPE: CAN!).

A. alpina (L.) Olin subsp. *attenuata* Greene var. *linearis* Hultén, Lunds Univ. Aarrskr. II. Sect. 2, 46: 1588. 1950. TYPE: Fort Yukon. *Murie 2204 fide* Ediger and Barkley (1978). Type not seen.

A. alpina (L.) Olin subsp. *attenuata* Greene var. *vestita* Hultén, Lunds Univ. Aarrskr. II. Sect. 2, 46: 1588. 1950. TYPE: Tonsina Lodge, eastern Pacific Coast district of Alaska. *Anderson 1989 fide* Ediger and Barkley (1978). Type not seen.

Arnica alpina (L.) Olin subsp. *iljinii* Maguire, Brittonia 4: 411. 1943. *A. iljinii* (Maguire) Iljin, Fl. URSS. 26: 658. 1961. *A. angustifolia* Vahl subsp. *iljinii* (Maguire) I. K. Ferguson in Heywood, Bot. J. Linn. Soc. 67: 282. 1973. TYPE: "Unterlauf des Jenissei, Ust-Jenisseiski Port (69° 39′ n. Br.) Aug. 4, 1926. *A. Tolmachev 199.*" (HOLOTYPE: LE, photo CAN!; ISOTYPES: GH!, O!).

Arnica intermedia Turcz., Bull. Soc. Nat. Mosc. 34: 203. 1851. *A. alpina* (L.) Olin subsp. *intermedia* (Turcz.) Maguire, Brittonia 4: 410. 1943. TYPE: Prope Alach-Jun 1835. *N. Turczaninow 836.* (HOLOTYPE: LE, photo CAN!).

Arnica sornborgeri Fern., Rhodora 7: 147. 1905. *A. alpina* (L.) Olin subsp. *sornborgeri* (Fern.) Maguire, Brittonia 4: 414. 1943. TYPE: "Rama, Labrador. Aug. 20–24, 1897. *J. D. Sornborger 157.*" (HOLOTYPE: GH!, photo CAN!; ISOTYPES: NY!, RM!, US!, photo CAN!).

Arnica terrae-novae Fern., Rhodora 27: 90. 1925. TYPE: "Green Gardens, Cape St. George, Newfoundland. July 24, 1922. *K. K. Mackenzie & L. Griscom 11039.*" (HOLOTYPE: GH, photo CAN!).

Arnica sornborgeri Fern. var. *ungavensis* Boivin, Nat. Can. 75: 211. 1948. *A. alpina* (L.) Olin var. *ungavensis* Boivin, Phytologia 23: 94. 1972. TYPE: Québec. Fort Chimo, Baie d'Ungava. Aug. 17, 1945. *Dutilly & Lepage 14768 fide* Ediger and Barkley (1978). Type not seen.

Arnica plantaginea Pursh, Fl. Amer. Sept. 527. 1814. *A. alpina* (L.) Olin var. *plantaginea* (Pursh) Ediger and Barkl., N. Amer. Fl. Ser. II, Pt. 10: 32. 1978. TYPE: "Labrador. Herb. Dickson. *Colmaster s.n.* (HOLOTYPE: PH!, photo CAN!).

Plants 0.5–5.4 dm tall; stems sparsely to moderately villous; lower cauline leaves 2–20 cm long, 0.3–4.1 cm wide, acute or acuminate, linear to broadly lanceolate, petioles short and broad-winged or narrow-winged and shorter than the blade, margins entire to irregularly denticulate or rarely dentate, glabrous to moderately villous; capitula 1–3 (–5); ligulate florets 6–16, 10–40 mm long, the teeth 0.2–7 mm long; periclinium moderately to densely pilose, white, stipitate-glands occasionally lacking or obscured; involucral bracts sparsely to moderately pilose; achenes 3.1 7 mm long; chromsome number $2n = 38, 57, 76, 95$.

DISTRIBUTION AND HABITAT. A circumpolar taxon, occurring between 49° and 83° N. Latitude in North America, between 60° and 80° N. in the U.S.S.R., and in northern Scandinavia near the Arctic Circle. In North America, its range extends from Alaska eastward through northern Manitoba, Ontario and Québec, with isolated populations in northern Newfoundland (Figure 5); exposed tundras, gravelly and rocky slopes, roadsides, moist banks and open woodlands. In the southernmost portion of its range it is found on alpine slopes and ridges. Flowers May to September.

5b. **Arnica angustifolia** Vahl subsp. **tomentosa** (Macoun) G. W. Douglas & G. Ruyle-Douglas, Canad. J. Bot. 56: 1710. 1978. *A. tomentosa* Macoun, Ottawa Nat. 13: 166. 1899. *A. alpina* (L.) Olin subsp. *tomentosa* (Macoun) Maguire, Madroño 6: 153. 1942. *A. alpina* (L.) Olin var. *tomentosa* (Macoun) Cronquist, Vas. Pl. Pac. N. W. 5: 46. 1955. TYPE: "Sheep Mountain, Waterton Lake, Rocky Mts., July 31, 1895. *J. Macoun 11606.*" (HOLOTYPE: CAN!, photo CAN!).

A. pulchella Fern., Rhodora 27: 18. 1915. TYPE: "Table Mountain. Region of Port au Port Bay, Newfoundland. July 16 and 17, 1914. *M. L. Fernald & H. St. John 10874.*" (HOLOTYPE: GH, photo CAN!; ISOTYPE: GH!, photo CAN!).

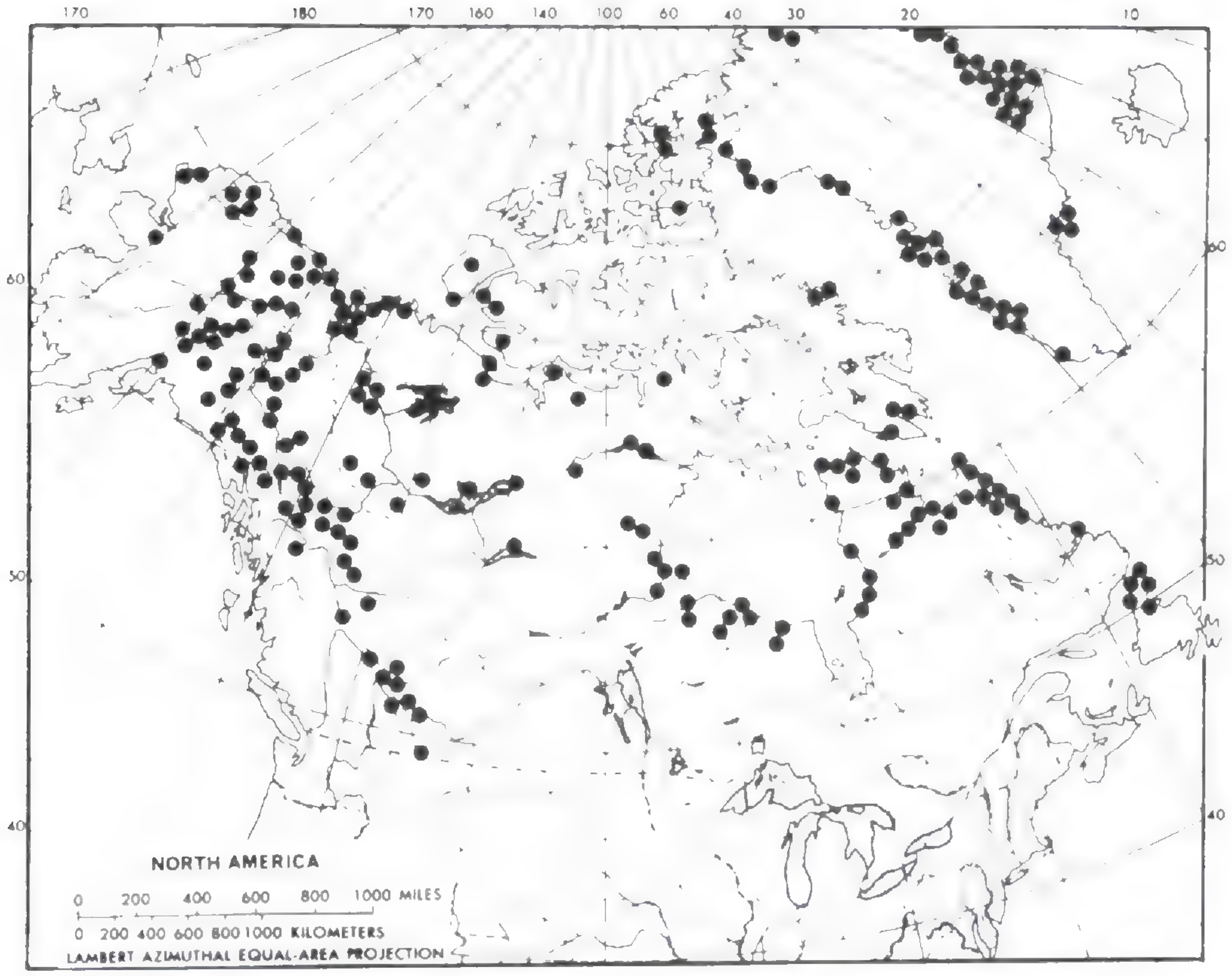


Figure 5. North American distribution of *Arnica angustifolia* subsp. *angustifolia*.

A. tomentosa Macoun ex Greene, Pittonia 4: 168. 1900. *non A. tomentosa* Macoun, Ottawa Nat. 13: 166. 1899. TYPE: "Mountains near Athabasca River near Lac Brule, Rocky Mts. June 20, 1898. *W. Spreadborough 19635.*" (ISOTYPE: CAN!, photo CAN!)

Plants 0.6–2 (–3) dm tall; stems densely villous, lower cauline leaves 3.5–10.5 cm long, 0.3–1.2 cm wide, acute, narrowly lanceolate, petioles short and broad-winged, margins entire or rarely irregularly denticulate, densely spreading woolly-villous; capitula 1 (–3); ligulate florets 7–12, 14.5–30 mm long, the teeth 0.5–3.5 mm long; periclinium densely woolly-villous and densely stipitate-glandular, white; involucral bracts densely woolly-villous; achenes 4.5–7.6 mm long; chromosome number $2n = 57, 76$.

DISTRIBUTION AND HABITAT. Infrequent in the Mackenzie delta region of the Northwest Territories, becoming more common southward in the Rocky Mountains of Alberta, British Columbia and Montana (Figure 6); bare rocky alpine slopes and subalpine meadows. Disjunct and infrequent in exposed rocky areas and dry limestone barrens of northwestern Newfoundland. Flowers July to August.

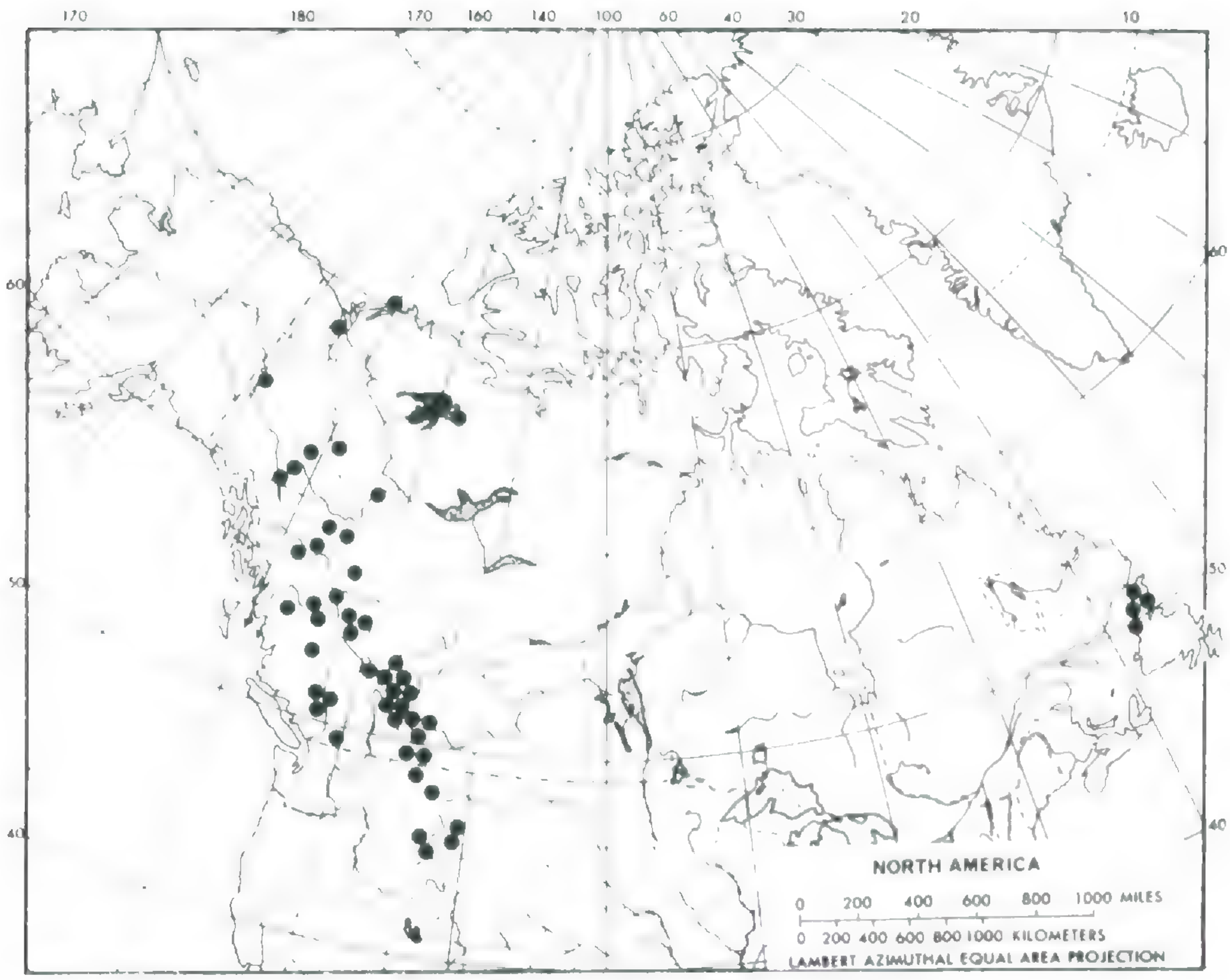


Figure 6. Distribution of *Arnica angustifolia* subsp. *tomentosa*.

6. **Arnica fulgens** Pursh, Fl. Amer. Sept. 527. 1814. *A. montana* var. *fulgens* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 164. 1818. TYPE: "On the banks of the Missouri" (Pursh 1814). (HOLOTYPE indicated by Maguire (1943) to be in BM was not found by staff; ISOTYPE, without locality, PH!, photo CAN!).

A. pedunculata Rydb., Bull. Torrey Bot. Club 24: 297. 1897. TYPE: "Flora of Central Montana, Spanish Basin, Madison Range. July 11, 1896. *J. H. Flodman 899.*" (HOLOTYPE: NY!).

A. monocephala Rydb., Mem. N. Y. Bot. Gard. 1: 435. 1900. *A. pedunculata* Rydb. var *monocephala* (Rydb.) Lunell, Amer. Midl. Nat. 5: 241. 1918. *A. pedunculata* Rydb. forma *monocephala* (Rydb.) Cockerell, Torreya 18: 183. 1918. TYPE: "Exploration of Montana and Yellowstone Park. Bridger Mountains, Mont. 14 June 1897. *P. A. Rydberg* and *E. A. Bessey 5221.*" (HOLOTYPE: NY!; ISOTYPE: CAN!).

A. pedunculata Rydb. var. *Tubularis* Cockerell, J. Hered. 7: 428. 1916. TYPE: "Boulder, Colorado. June 1915. *W. P. Cockerell s.n.*" (HOLOTYPE: GH!).

Plants 1 7.2 dm tall; rhizomes short, densely scaly, thick; stems solitary or few, simple, moderately puberulent becoming increasingly pubescent upwards, stipitate-glandular, base with conspicuous dense tufts of long brown woolly hair in axils of basal leaves and

persistent leaf bases; leaves 3 5 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 4.5 20 cm long, 0.6 2.5 cm wide, obtuse, narrowly oblong to oblanceolate, petioles narrow or broad-winged and shorter than the blade, margins entire or sometimes irregularly remotely denticulate, moderately uniformly pubescent, stipitate-glandular, 3-5 nerved; capitula erect. 1 (3), broadly hemispheric, 14-30 mm wide, 11 17 mm long; periclinium moderately to densely pilose, white, stipitate-glandular; involucral bracts 13–21, 10–15.5 mm long, 1.5–4.5 mm wide, narrowly to broadly lanceolate to elliptic-oblong, obtuse to occasionally acute, uniformly pilose throughout, the tips pilose within, stipitate-glandular; ligulate florets 8 16, dark orange-yellow, 16 32 mm long, 2.9–8 mm wide, 3-toothed, the teeth 0.3 2.1 mm long; disc florets 6-9.1 mm long, goblet-shaped, stipitate-glandular, densely pilose, the tube 2.5–5 mm long; achenes 3.5-7 mm long, densely hirsute throughout, occasionally sparingly glandular; pappus white or nearly so; chromosome number $2n = 38$.

DISTRIBUTION AND HABITAT. Throughout interior British Columbia and southern Alberta extending north into the Peace River drainage area, southern Saskatchewan, southwestern Manitoba, south to northern California, northern Nevada, northern Utah, northern Colorado, and east to western North and South Dakota (Figure 7); prairies and grasslands at low elevations in the northern part of the range, montane up to 3,000 meters in Wyoming and Colorado. Plants commonly found in moist depressed areas, often growing in dense clumps. Flowers May to July.

Arnica fulgens is a densely rhizomatous species occupying montane to grassland habitats throughout the northerm United States and adjacent southwestern Canada. It is distinguished by having a large broadly hemispheric capitulum, entire leaves, dense axillary tufts of brown woolly hairs at the base of the stem, and dense glandless hairs on the disc corollas. A discussion of the taxonomic history and synonymy of *A. fulgens* and *A. sororia,* is presented in Downie and Denford (1987).

7. **Arnica sororia** Greene, Ottawa Nat. 23: 213. 1910. *A. fulgens* Pursh var. *sororia* (Greene) G. W. Douglas and G. Ruyle-Douglas in Taylor and MacBryde, Canad. J. Bot. 56: 185. 1978. TYPE: "Near International boundary between Kettle and Columbia rivers. Cascade, B.C. June 30, 1902. *J. M. Macoun (Geol. Surv. Can. No. 64987).*" (HOLOTYPE: ND!; ISOTYPES: CAN!, GH!, photos CAN!, UC!).

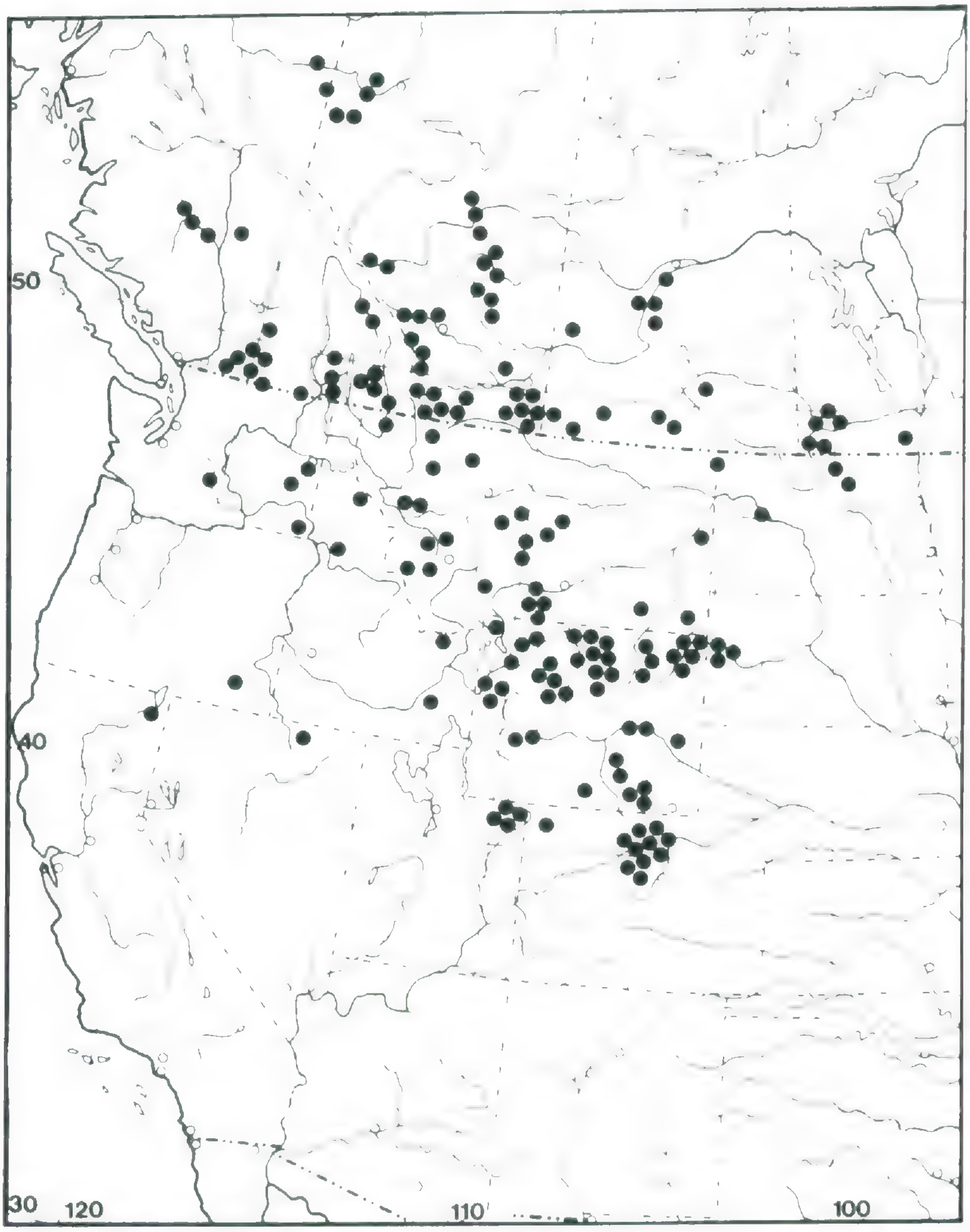


Figure 7. Distribution of *Arnica fulgens*.

A. stricta Greene, Ottawa Nat. 23: 214. 1910, non *A. stricta* A. Nels., Ottawa Nat. 23: 214. 1910. *A. trinervata* Rydb., N. Amer. Fl. 34: 344. 1927. TYPE: "Near International Boundary between Kettle and Columbia Rivers. June 30, 1902. *J. M. Macoun (Geol. Surv. Can. No. 64979).*" On isotypes: "W. of Cascade, B.C." (HOLOTYPE: ND!, ISOTYPES: CAN!, NY, photos CAN!, UC!).

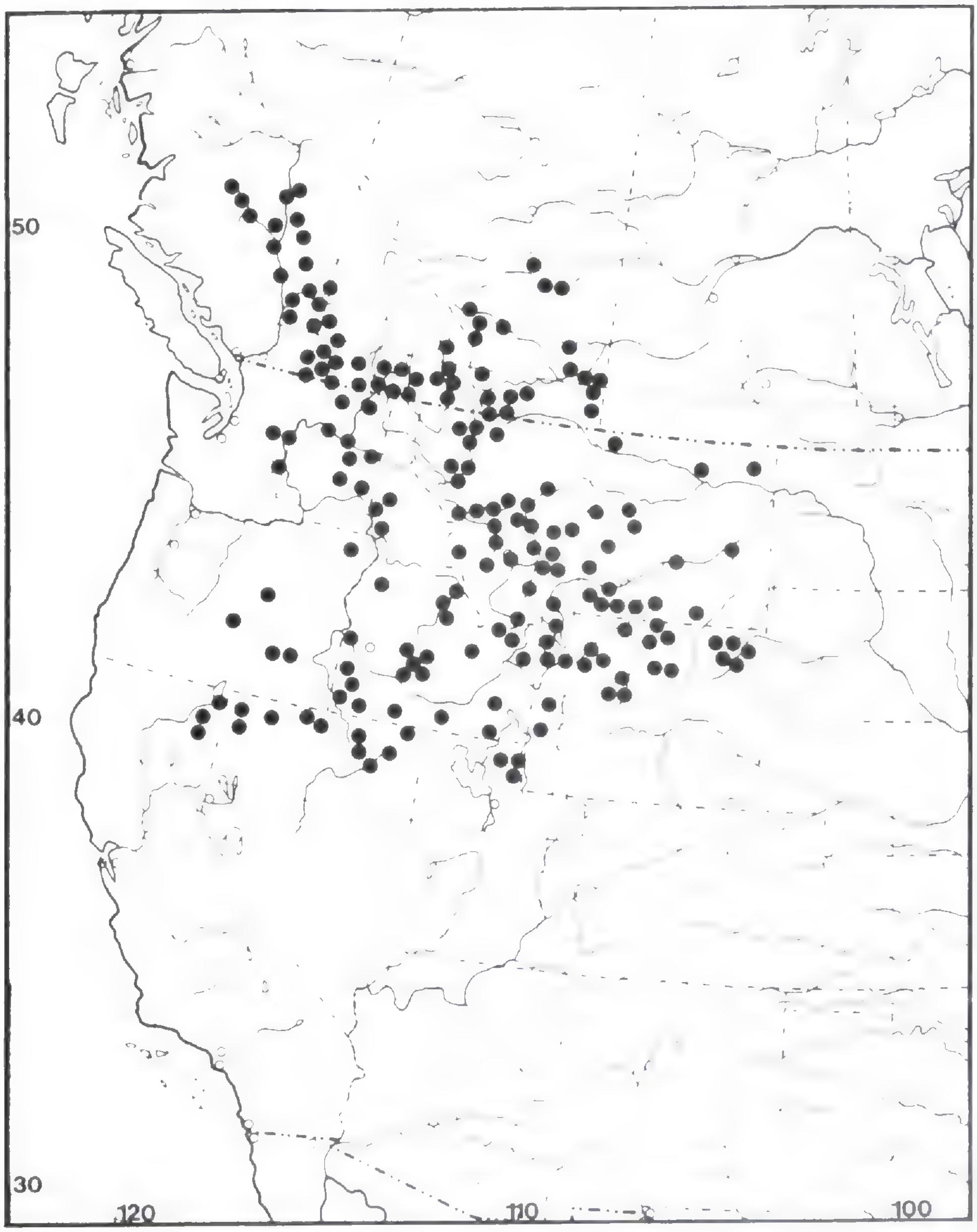


Figure 8. Distribution of *Arnica sororia*.

Plants 1.5–5 dm tall; rhizomes short, less scaly than in *A. fulgens*, slender; stems solitary or few, simple to branched, base lacking axillary tufts of brown hair, occasionally with few whitish hairs or none at all, moderately puberulent below becoming increasingly pubescent upwards, stipitate-glandular; leaves 3–6 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 3.5 14.5 cm

long; 0.6–2.4 cm wide (usually narrower than in *A. fulgens*), obtuse, narrowly oblong to oblanceolate, the petioles narrow-winged and shorter than the blade, margins entire to sometimes irregularly remotely denticulate, moderately uniformly pubescent, short stipitate-glandular, 3–5 nerved; capitula erect, 1–5, broadly hemispheric, 11–27 mm wide, 9–17 mm long; periclinium moderately to densely pilose, white, stipitate-glandular; involucral bracts 13–20, 9.5–14.2 mm long, 1.2–3.1 mm wide, narrowly to occasionally broadly lanceolate, acute, uniformly pilose throughout, tips not at all pilose within, glandular; ligulate florets 9–17, dark orange-yellow, 15–31 mm long, 2.5–7.5 mm wide, 3-toothed, the teeth 0.2–1.8 mm long; disc florets 6.9–10 mm long, goblet-shaped, stipitate-glandular, not at all pubescent, the tube 3–5.5 mm long; achenes 3–5.5 mm long, densely hirsute throughout, occasionally sparingly glandular; pappus white or nearly so; chromosome number $2n = 38$.

DISTRIBUTION AND HABITAT. Throughout the interior of southern British Columbia, southern Alberta, south to northern California, northern Nevada, northern Utah and east to northwestern Wyoming and eastern Montana (Figure 8); prairies and grasslands at low elevations particularly in very dry areas; in less dense populations, in drier habitats and at lower elevations than *Arnica fulgens*. Flowers May to July.

ACKNOWLEDGMENTS

Financial support from the Boreal Institute of Alberta for Northern Studies to S. R. D. and a Natural Sciences and Engineering Research Council of Canada grant to K. E. D. are gratefully acknowledged. we also thank the curators and staff of the following herbaria for supplying loans of material and/or accommodating visits: ALA, ALTA, BRY, C, CAN, DAO, GH, ICEL, LE, MONT, MT, ND, NY, O, PH, RENO, RM, SASK, UBC, UC, and US.

LITERATURE CITED

AFZELIUS, K. 1936. Apomixis in der gattung *Arnica*. Svensk Bot. Tidskr. 30: 572–579.

BÖCHER, T. W., AND K. LARSEN. 1950. Chromosome numbers of some arctic or boreal flowering plants. Meddel Grønland 147: 1–32.

DOUGLAS, G. W., AND G. RUYLE-DOUGLAS. 1978. Nomenclatural changes with respect to the Asteraceae of British Columbia. 1. Senecioneae. Canad. J. Bot. 56: 1710–1711.

Downie, S. R. 1985. Chromosome Number Reports LXXXVIII. Taxon 34: 550.
———. 1988. Morphological, cytological and flavonoid variability of the *Arnica angustifolia* aggregate (Asteraceae). Canad. J. Bot. (in press)
Downie, S. R., and K. E. Denford. 1986a. The taxonomy of *Arnica frigida* and *A. louiseana* (Asteraceae). Canad. J. Bot. 64: 1355–1372.
———, and ———. 1986b. The flavonoids of *Arnica frigida* and *A. louiseana* (Asteraceae). Canad. J. Bot. 64: 2748–2752.
———, and ———. 1987. The biosystematics of *Arnica fulgens* and *A. sororia* (Asteraceae). Canad. J. Bot. 65: 559–570.
———, and ———. 1988. Flavonoid variation in *Arnica* subgenus *Arctica*. Biochem. Syst. Ecol. (in press)
Ediger, R. I., and T. M. Barkley. 1978. *Arnica* pp. 16–44. *In:* North American flora, Series II. Part 10. C. T. Rogerson, Ed. New York Botanical Garden, New York.
Fernald, M. L. 1933. Recent discoveries in the Newfoundland flora. Rhodora, 35: 364–369.
Grant, V. 1971. Plant Speciation. Columbia University Press, New York.
Gustafsson, A. 1947. Apomixis in the higher plants. III. Biotype and species formation. Acta Univ. Lund 44: 183–370.
Maguire, B. 1943. A monograph of the genus *Arnica*. Brittonia, 4: 386–510.
Ornduff, R., T. Mosquin, D. W. Kyhos, and P. Raven. 1967. Chromosome numbers in Compositae VI, Senecioneae II. Amer. J. Bot. 54: 205–213.
Rydberg, P. A. 1927. *Arnica,* Carduaceae: Senecioneae. North American Flora, Vol. 34(4): 321–357.
Taylor, R. L., and R. P. Brockman. 1966. Chromosome numbers of some western Canadian plants. Canad. J. Bot. 44: 1093 1103.
Wolf, S. J., and K. E. Denford. 1984. Taxonomy of *Arnica* (Compositae) subgenus *Austromontana*. Rhodora 86: 239 309.

S. R. D.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF OTTAWA
OTTAWA, ONTARIO K1N 6N5
CANADA

K. E. D.
DEPARTMENT OF BOTANY
UNIVERSITY OF ALBERTA
EDMONTON, ALBERTA T6G 2E9
CANADA

RHODORA, Vol. 90, No. 863, 1988

TAXONOMY OF *SENECIO STREPTANTHIFOLIUS* GREENE

JOHN F. BAIN

ABSTRACT

Seven varieties of *Senecio streptanthifolius* Greene are recognized based on morphological characters, flavonoids and chromosome numbers. Four new combinations are made and two new varieties described. The results of a cluster analysis incorporating morphological and flavonoid characters are compared with those from one using only morphological characters. The addition of flavonoid characters permits a better definition of taxa in most cases.

Key Words: *Senecio streptanthifolius*, taxonomy, flavonoids, phytogeography, North America

INTRODUCTION

The treatments of *Senecio streptanthifolius* Greene have all been in agreement that the species includes numerous variants. Greenman (1916, as *S. cymbalarioides* Nutt.) recognized three varieties. He described var. *borealis* (T. & G.) Greenm. as having "subspatulate to oblanceolate lower leaves" rather than the "broadly ovate, obovate to somewhat spatulate leaves" of the typical variety, and var. *streptanthifolius* (Greene) Greenm. as having "suborbicular, obovate or oblong-ovate, somewhat glaucous leaves." Barkley (1962, 1978) considered the species to consist of numerous semi-distinct phases none of which was worth formal recognition. Like Greenman, he cited leaf characters as important for distinguishing groups. Recent information on chromosome numbers indicates that the species includes at least two ploidy levels (Morton, 1981; Bain, 1985) and flavonoid studies (Bain and Denford, 1985) support the recognition of some of the variants described by previous authors. What remains to be done is to relate the findings of these recent studies to the more classical morphological analyses of Greenman and Barkley.

The present phenetic analysis was undertaken to determine whether additional morphological characters exist that are useful for separating the variants within the *Senecio streptanthifolius* complex. The results of this analysis, presented here, were combined with those of the aforementioned chromosome and flavonoid studies as well as already established morphological data and used as the basis for a revision of the species complex.

METHODS

Specimens of *Senecio streptanthifolius* were collected from throughout the species range as were related species from the same region. In addition, herbarium specimens from ALTA, BM, BRY, CAN, CAS, COLO, DAO, DS, F, GH, JEPS, MO, NDG, NY, OSC, PENN, PH, RM, TEX, UC, US, UTC were used to provide a more complete basis of comparison within the complex. Specimens included in the analysis were annotated according to views which have been expressed with some consistency in past literature. The taxa recognized initially included the phases described in 1962 by Barkley (*streptanthifolius, rubricaulis, platylobus, leonardi* (including *molinarius*), *suksdorfii, laetiflorus*), a segregate named by Rydberg *S. acutidens*, and the diploid (*borealis* 2×) and tetraploid (*borealis* 4×) collections of *borealis* (*sensu* Greenman). Along with these taxa were included representative specimens of *S. pauperculus, S. canus, S. multilobatus, S. neomexicanus,* and *S. fendleri.* A total of eighty-five representative specimens was chosen for inclusion in the analysis. The specimens were mostly taken from my own collections because they were unmounted and therefore most easily measured. When necessary, mounted herbarium specimens were added to augment the sample size of each taxon.

Thirty-two structural characters were scored for the operational taxonomic units (OTUs) chosen (Table 1). In addition, eight flavonoid characters as described previously (Bain and Denford, 1985) were included in the analysis.

Some leaf characters were measured using a digitizing tablet and a measurement program written by M. R. T. Dale of the University of Alberta. Leaves were scored by xerographing the leaf shape onto a clear acetate sheet and then projecting the image onto the digitizer surface. The shape was then accurately recorded and the measurements corrected for magnification. In addition to calculating the leaf area, leaf perimeter, basal leaf angle, maximum leaf width, distance of the maximum width from the apex, the total leaf length, the ratio of these last two values and the ratio of leaf length to width, the program drew a polygon joining the outermost points of each leaf. The program then calculated ratios for the leaf area/polygon area and for leaf perimeter/polygon perimeter. Each ratio is a measure of the entirety of the leaf, although the two are inversely related.

Table 1. Morphological characters used in cluster analysis.

1. Root Type (0–2; 0 = tap, 2 = fibrous)	17. Head Diameter (excluding ray)
2. Stalk Ht.	18. Pappus Length
3. Leaf Pubescence (0–3; 0 = glabrous)	19. Disc Corolla Length
4. Leaf Margins (basal)	20. Anther Length
5. Leaf Margins (apical)	21. Ray Corolla Length
6. Petiole Length	22. Disc Floret No.
7. Cauline Leaf No.	23. Ray Floret No.
8. Cauline Leaf Base (clasping/entire)	24. Phyllary Length
9. Cauline Leaf Margins (entire/lobed)	25. Phyllary No.
10. Head No.	26. Leaf Perimeter
11. Secondary Stalks No.	27. Basal Leaf Angle
12. Stalk No.	28. Max. Leaf Width
13. Involucre Pubescence (upper)	29. Distance/Leaf Length Ratio
14. Involucre Pubescence (lower)	30. Total Leaf Length
15. Involucre Length	31. Perimeter (leaf/polygon) Ratio
16. Involucre Width (bottom)	32. Leaf L/W Ratio

Two distinct cluster analyses were performed. The first included the thirty-two morphological characters and the eight flavonoid characters. The second included only the morphological characters. The cluster analyses were performed using the TAXMAP classification program (Carmichael, 1980). The program calculates the ranges of the variables, normalizes the raw data as fractions of the range, then calculates a relative proximity between each pair of OTUs. An option that allows for the weighting of characters was not exercised. Results of the analysis are displayed in the form of a taxometric map (Carmichael and Sneath, 1969). The map is a two-dimensional representation of the multidimensional hyperspace occupied by the OTUs. Circles (representing clusters) and points (representing unclustered OTUs) are joined by lines representing the undistorted phenetic distances between the clusters. Taxometric maps may be either generated through the use of a plotter by the program directly, or drawn by hand using coordinates supplied by the program. Both methods were employed although only hand-drawn maps are presented.

RESULTS

Eighteen clusters and twenty-one isolated OTUs were separated in the first analysis using all characters. The computer-generated, complete taxometric map is difficult to interpret because of the large

number of overlapping clusters and adjoining lines. For this reason the map was re-drawn by hand from the same data but with only clusters 1–18 (those with >1 OTU) and their nearest neighbor distances included. This simplified map is shown in Figure 1. As indicated in the Figure, the clusters can be divided into four groups (A–D) based on the following explanation.

It is apparent that there are two major clusters (#1 and #3), which are each other's nearest neighbor. Of the remaining sixteen clusters, only six do not have either cluster #1 or #3 as its nearest neighbor.

Based upon these nearest neighbor relationships, the clusters themselves form two major groups, the cores of which are clusters #1 and #3 respectively.

The group centered around cluster #1 (Group A) consists mostly of specimens of the *suksdorfii* and *laetiflorus* phases, as well as two of the three *borealis* 4× specimens included in the analysis. The group centered around cluster #3 (Group B) includes mostly *borealis* and *streptanthifolius* specimens.

In addition to these two major groups, two other groups may be defined using "nearest neighbor" relationships. Clusters #10 and #18 both have cluster #2 as their nearest neighbor. All three clusters (#2, #10, #18) contain specimens with dissected leaves referable or related to the *rubricaulis–platylobus* phases of Barkley. These clusters comprise Group C.

The final group (Group D) comprises two clusters (#8 and #11) both containing tomentose specimens, most of which belong to the *leonardi–molinarius* phases. Groups B and D are closely related as evidenced by the fact that the nearest neighbor of cluster #8 is cluster #3 (the core cluster of group B). These two groups are much more easily separated when flavonoid characters are omitted from the analysis as will become apparent after examination of the results of analysis #2.

The four groups delimited by the first analysis are also evident in the second analysis (Figure 2), although only structural characters were included. The groups are, however, not so well defined. Group A is still largely composed of *suksdorfii* and *laetiflorus* individuals but includes also a few *borealis* and *rubricaulis* individuals. Group B still contains only *streptanthifolius* and *borealis* individuals but the internal segregation of the two is not as clear as in the first analysis. The separation of Group B and Group C is not as clear, as evidenced by the increased number of *streptanthifolius* specimens

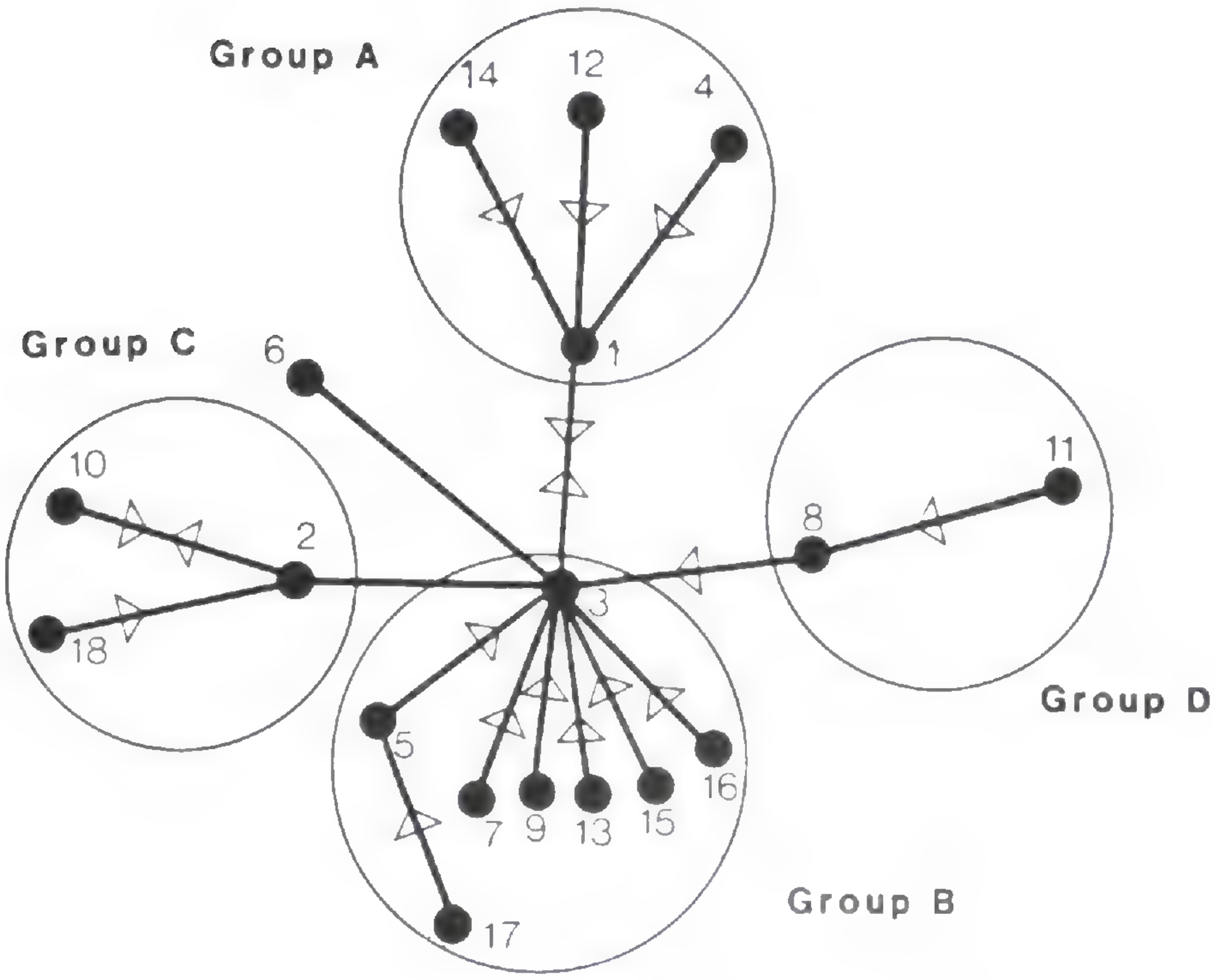


Figure 1. Nearest neighbor diagram of analysis #1 (combined structural and flavonoid characters). Numbers refer to those clusters identified in the analysis which contained >1 OTU. Groups A D represent morphologically distinct groups as outlined in the text.

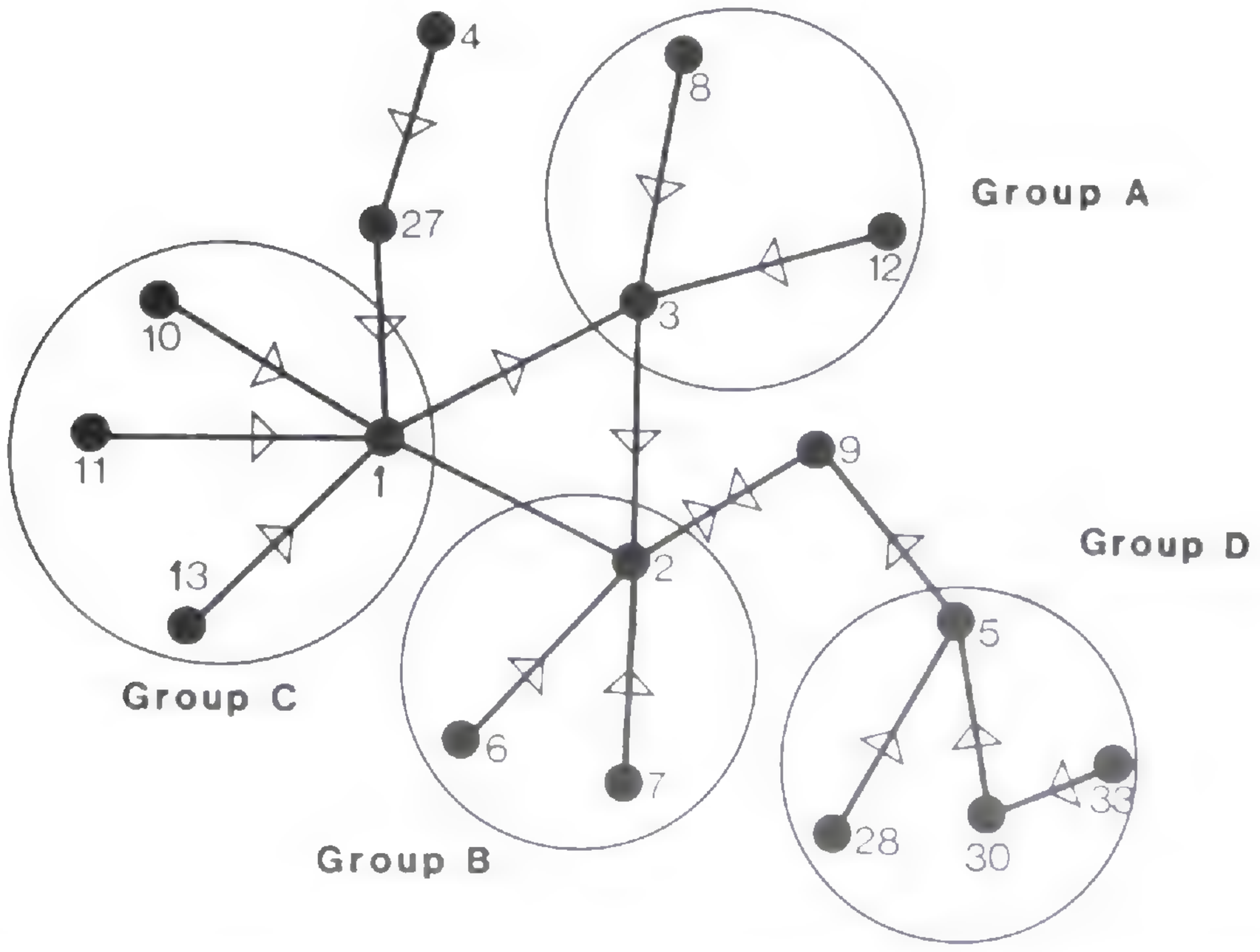


Figure 2. Nearest neighbor diagram of analysis #2 (structural characters only).

included in Group C. The separation of Group C from *S. multilobatus* individuals (clusters #4 and #27) is also less clear in this analysis. The tomentose specimens (Group D) cluster as well as or better than in analysis #1. Group D is connected to the rest of the clusters through a small cluster (#9) containing two tomentose specimens of uncertain affinities.

A comparison of the two analyses demonstrates that flavonoid characters are useful for clarifying definition of the groups in most cases, but it also demonstrates that the groups are delimited on the basis of morphology alone.

Not only are the four major groups recognizable in each analysis, but within the groups, the separation of individuals follows the same patterns. Within Group A in both analyses some of the *laetiflorus* specimens form a cluster distinct from the *suksdorfii* specimens. This pattern supports Barkley's separation of the two phases, but at the same time demonstrates a relationship between the two which was previously not apparent. In Group B, *borealis* specimens cluster separately from *streptanthifolius* specimens. This pattern supports Greenman's separation of the two taxa as distinct varieties and they are further distinguished when chemical characters are included. Groups C and D show no discernible sub-groups.

In no case do the *borealis* 2× and *borealis* 4× specimens cluster together.

DISCUSSION

The results clearly support recognition of infraspecific taxa within the complex and variable *Senecio streptanthifolius*. However, without the incorporation (and interpretation) of flavonoid data, the variation pattern revealed in the taxmaps is difficult to incorporate into a useful formal classification. As mentioned above, the core clusters (#1 and #3) of groups A and B are, in fact, each other's nearest neighbor. This proximity hides the fact that the two groups are approximately the same as the two major sub-groups within the species when defined using flavonoid characters alone (Bain and Denford, 1985). Groups A and B also have distinct but contiguous distribution patterns; Group A (*streptanthifolius-borealis*) occurs in the Rocky mountain region while Group B (*laetiflorus-suskdorfii*) is restricted to more western montane and alpine regions. Once Groups A and B are recognized as distinct, it is easy to separate taxa

within each group. Within Group A, *streptanthifolius* and *borealis* are easily separable based on morphology and distribution differences. Within Group B, *laetiflorus* is easily separable from *suksdorfii* on morphological (size and inflorescence numbers) and habitat differences.

The interpretation of the position of group C as part of *Senecio streptanthifolius* but allied with *S. multilobatus* is supported by the results of this study, as is the existence of a tomentose phase (Group D) distinct from *S. neomexicanus* and *S. canus*.

Thus, based on these and previously reported results, seven varieties of *Senecio streptanthifolius* are recognized in the present treatment: var. *streptanthifolius*, var. *borealis*, var. *rubricaulis*, var. *laetiflorus*, var. *kluanei* (= *borealis* 4×), var. *wallowensis* (= *suksdorfii*), and var. *oodes* (= *leonardi-molinarius*). The nomenclatural changes are discussed in the taxonomy section below.

Senecio streptanthifolius remains a complex species but the formal treatment of the phases as varieties presents a more logical means of dealing with the variation encountered. For the most part the varieties are chemically, geographically and ecologically distinct. While they are also usually morphologically distinct, there remain numerous individuals not readily referable to a particular variety.

PHYTOGEOGRAPHY

The interspecific relationships characteristic of the aureoid species complex were most certainly forged, at least in part, by past geologic events and climatic changes. Both Barkley (1962) and Kowal (1975) presented brief synopses of the effects of post-glacial events upon distribution of the aureoid taxa that they studied. Barkley (1988) presents a more detailed account. Barkley's discussions also included views on how the constantly changing patterns of overlap among species distributions, coupled with subsequent introgression, has contributed to the evolution of species within the group. The following discussion is similarly intended to present an overview of historical events that have shaped the *Senecio streptanthifolius* complex.

The current distributions and ecological preferences exhibited by many contemporary aureoid species suggest that the group had its origin as part of a Tertiary assemblage of plants (mixed mesophytic forest) analogous to contemporary hardwood deciduous forests.

The paucity of aureoid *Senecio* species in Europe and Asia (Tutin et al., 1976; Schishkin, 1961) supports this idea, suggesting that the aureoids were never circumboreal and that they originated somewhere in North America. According to Wolfe (1978), the Mixed Mesophytic Forests were not widely distributed in North America until the Miocene, when the exchange of warm temperate plants between Asia and North America via Beringia was reduced or had stopped. Conversely, the Miocene boreal forests are thought to have been Holarctic (Matthews, 1979), suggesting that a boreal origin for the aureoid *Senecio* species would have resulted in a greater species representation in contemporary Asian and European floras.

The current distribution pattern of *Senecio streptanthifolius* var. *streptanthifolius* suggests that it may have once been more widespread but has since had its range reduced so that it now occupies higher regions in the southwestern Rockies, the Sierra Nevada and some of the ranges in between (i.e., the Ruby and Jarbidge Mts. in Nevada). This range reduction may have occurred during the late Pliocene with the onset of warmer and drier conditions, especially in the rain shadows of the Sierra Nevada and the Cascades. The initial separation of *S. streptanthifolius* from other aureoid species must have occurred earlier.

During the Pliocene, those more xerophytic species such as *Senecio neomexicanus, S. canus* and *S. multilobatus* also evolved in response to drier conditions. Gene flow between these species and *S. streptanthifolius* probably occurred more recently, during the glaciations of the Pleistocene and the hypsithermal of the Holocene, as a result of migration and range overlap. During this time, timberlines in the Great Basin have been estimated to have been lowered by 600–1200 metres (Billings, 1977). *Senecio streptanthifolius* var. *oodes*, var. *rubricaulis*, and var. *kluanei* are all thought to have evolved during the Pleistocene. The latter (var. *kluanei*), however, has a very different range from the other two taxa. Its proximity to unglaciated areas in the Yukon suggests that its origin may be implicated more directly with continental Pleistocene glaciation. Displacement of taxa into or within unglaciated portions of the Yukon Territory may have occurred with subsequent hybridization and polyploidy, producing new taxa such as var. *kluanei*. These plants have subsequently migrated to glaciated areas, as can been seen from the distribution map (Figure 3). Possible origins for var. *kluanei* were discussed (under the name *borealis* 4×) by Bain and Den-

ford (1985). Finally, based on distribution data, the emergence of *S. streptanthifolius* var. *borealis* seems to be directly correlated with the onset of glacial retreat at the beginning of the Holocene. Hultén (1937) designated a number of species with this same distribution pattern as "continental western radiants."

The origins of the remaining two varieties, var. *wallowensis* and var. *laetiflorus*, are more obscure. Besides sharing flavonoid characters, the two species have similar distributions. Both are restricted to areas west of the Rocky Mountains, primarily in Oregon, and both extend only as far south as Mt. Rose, Nevada. It is therefore presumed that both taxa evolved from the same or a similar ancestor. Cooling temperatures during the Pliocene expanded alpine habitats in the Wallowa mountains, and var. *wallowensis* may have evolved there via ecological isolation (*sensu* Stebbins, 1950) whereby peripheral populations in alpine or subalpine habitats gradually diverged from their ancestral types. The uplift of the Cascade Mountains during this same period resulted in the drying of what is now interior Oregon and north-central California, including previously existing lakes, and erosion of the lava beds covering the area. The alkaline conditions that resulted persist in the mesic alkaline meadows occupied by var. *laetiflorus* today, so presumably var. *laetiflorus* evolved in this region at approximately the same time var. *wallowensis* evolved in response to cooling conditions at higher altitudes.

The disjunct distribution of var. *wallowensis* remains difficult to explain. Presence of this species on Mt. Rose but not on peaks of the neighboring Sierra Nevada may be the result of edaphic differences. Billings (1950) stressed the importance of such differences between the Sierra Nevada and the neighboring Carson (including Mt. Rose) and Virginia ranges in determining the different floristic elements of the two ranges. Whether this Mt. Rose - Wallowa Mts. disjunction is the result of dispersal or vicariance is unclear. For the present, the fact that var. *wallowensis* occurs at both the southern and the northern extremes of the range of var. *laetiflorus* is interpreted as evidence of a previous, more contiguous distribution for var. *wallowensis* and that both var. *laetiflorus* and var. *wallowensis* evolved at about the same time (early to mid-Pliocene) from a common ancestor whose range combined the current ranges of the two varieties.

TAXONOMY

Senecio streptanthifolius Greene Erythea 3: 23. 1895.

Herbaceous perennial, (0.9)2–5(6) dm tall, glabrous or with pubescence in the axils of leaves or lightly floccose-tomentose to variously glabrescent on leaf surfaces, especially the lower surface or at the bases of the involucres. Stems 1–3 arising from a single basal rosette; rootstock various, ranging from a taproot to a fibrous root, often giving rise to a stout branching caudex. Basal leaves turgid and leathery, petiole (1.5)2.5–7(9) cm long, blade variable, oblanceolate to obovate to widely obovate, base obtuse to cuneate, margins usually entire in the lower 2/3 of the blade, dentate or serrate-dentate to crenate near the apex, or occasionally deeply dissected in the lower portion with a prominent terminal lobe, (1.1)1.5–5(9) cm long, 0.8–2.8(3.5) cm wide; cauline leaves normally reduced, the lower ones resembling the basal leaves but usually more dissected or bract-like. Inflorescence a loose corymbiform cyme of (3-)8–20(-30) heads; involucral bracts ca. 13 or ca. 21, (4-)4.5–7(-9) mm long; achenes glabrous. $n = 23, 46$.

KEY TO THE VARIETIES OF *SENECIO STREPTANTHIFOLIUS*

1. Margins of the basal leaves evenly dentate to serrate for the whole perimeter of the leaf, not entire at the base. Involucre glabrous or tomentose to densely floccose-tomentose at the base, often floccose-tomentose throughout. ..... 2.
   2. Leaf blades tomentose, obovate, ovate or widely ovate; leaf base cuneate or obtuse. Colorado, uncommon in Wyoming and Nevada. ..... **7.** var. *oodes*.
   2. Leaf blades glabrous, obovate to widely oblanceolate; leaf base cuneate to narrowly cuneate. Yukon and northern British Columbia. ..... **3.** var. *kluanei*.
1. Margins of the basal leaves either entire at the base, unevenly deeply dentate or lobate. Involucre glabrous. ..... 3.
   3. Basal leaves obtuse, truncate or subcordate at the base; blade widely ovate to orbicular; heads 3–7. Alpine to sub-alpine, primarily of the Wallowa Mts., Oregon and Mt. Rose, Nevada. ..... **6.** var. *wallowensis*.
   3. Basal leaves cuneate to attenuate or obtuse at the base; blade ovate to oblanceolate to subspatulate; heads 6–20+; mesic, wooded slopes and meadows throughout temperate western North America. ..... **4.**

4. Disc florets 45–85; leaves turgid and thickish, not obviously shiny or leathery in texture. ..... 5. var. *laetiflorus*.
4. Disc florets 25–45; leaves thick, shiny and leathery in texture. ..... 5.
5. Basal leaf margins dissected, either lobed or deeply serrate-dentate; disc floret corolla 6–7 mm long; cauline leaf margins lobed to pinnatisect. ..... 4. var. *rubricaulis*.
5. Basal leaf margins generally sub-entire, or at most dentate to serrate-dentate at apex; disc floret corolla 4.5–6.0 mm long; cauline leaves usually sub-entire, often reduced and bract-like. ..... 6.
6. Leaf blades obovate to widely obovate, often 2 × longer than wide. Western U.S., extending into southern British Columbia. ..... 1. var. *streptanthifolius*.
6. Leaf blades oblanceolate to sub-spatulate, 2.5–3× longer than wide. Western and northern Canada, as far north as southern Yukon and Northwest Territories. ..... 2. var. *borealis*.

1. **Senecio streptanthifolius** Greene var. **streptanthifolius** TYPE: "on dry, wooded banks in Beaver Canyon, Idaho...collected by the writer in August 1889 and distributed under the wrong name of *S. rapifolius*" *Greene s.n.* (HOLOTYPE: NDG!; ISOTYPES: UC! DH!). *Senecio cymbalarioides* var. *streptanthifolius* (Greene) Greenm., Ann. Missouri Bot. Gard. *3*:117. 1916. Figures 3 and 4.

Senecio cymbalarioides Nutt.(*non* Buek), Trans. Am. Phil. Soc. (ii) 7:412. 1841. TYPE: "in Oregon." *Nuttall s.n.* (HOLOTYPE: BM!).

Senecio adamsii Howell (*non* Cheeseman), Fl. N.W. Am. 1:379. 1900. *Senecio suksdorfii* Greenm., Bot. Gazette 53:511. 1912. TYPE: "by the base of cliffs, Mt. Adams Washington." *Howell s.n.* (ISOTYPE: OSC!).

Senecio longipetiolatus Rydb., Bull. Torrey Bot. Club 27:176. 1900. TYPE: "Wyoming: Spread Creek, Teton Forest Reserve, 1897, *F. Tweedy 585* (type in the herbarium of N.Y. Botanical Garden)" (HOLOTYPE: NY!).

Senecio fulgens Rydb., Bull. Torrey Bot. Club 27:177. 1900. *Senecio rydbergii* A. Nelson in Coulter and Nelson Man.: 582. 1909. TYPE: "Wyoming: Grand Creek, Teton Forest Reserve, 1897, *F. Tweedy 584* (type in the herbarium of the N.Y. Botanical Garden)" (HOLOTYPE: NY!).

Senecio subcuneatus Rydb., Bull. Torrey Bot. Club 27:179. 1900. TYPE: "Colorado: Grizzly Peak, 1896. *C. F. Baker s.n.* (type in the herbarium of N.Y. Botanical Garden)" HOLOTYPE: NY!).

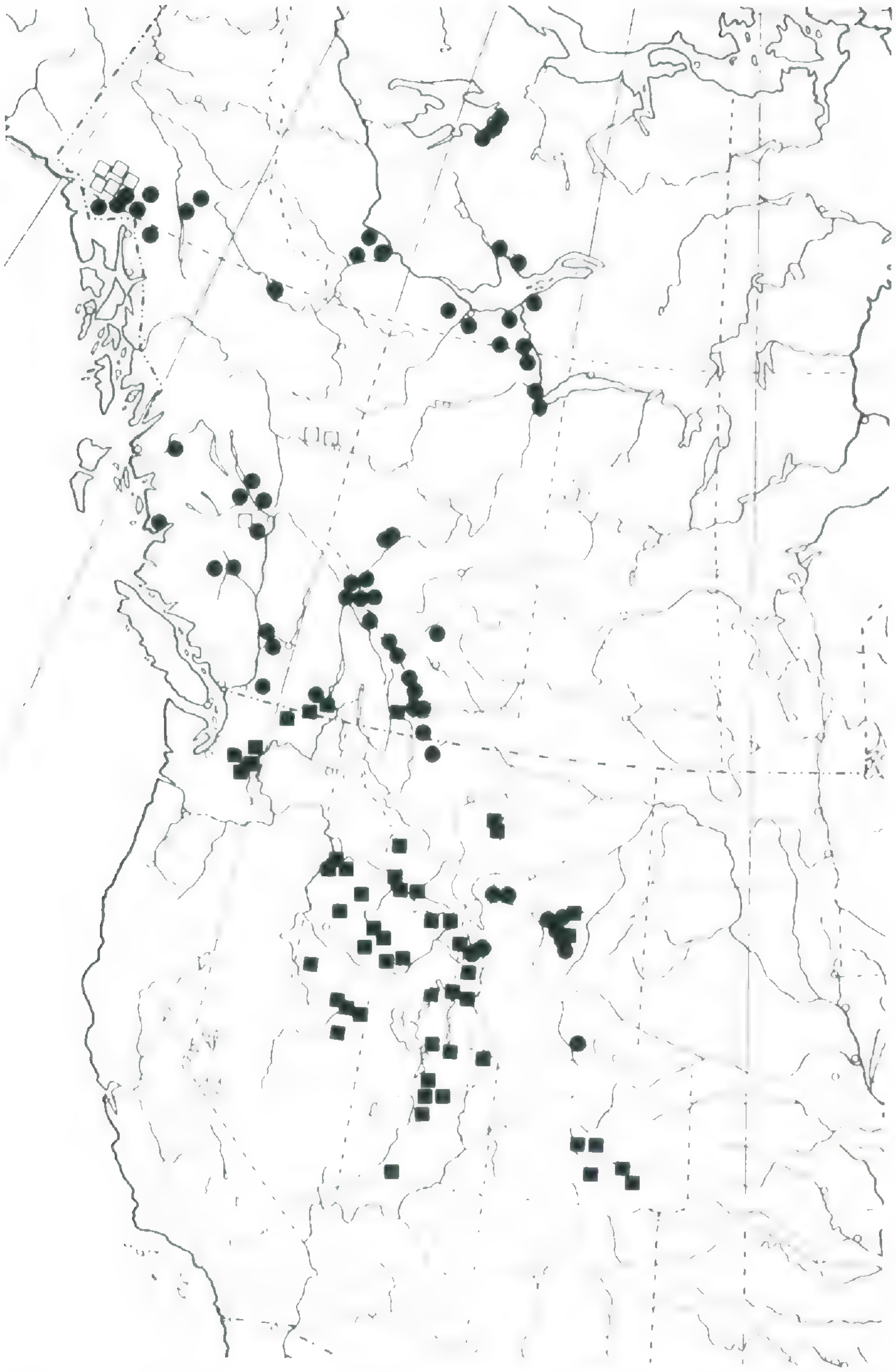


Figure 3. Distribution of *Senecio streptanthifolius* var. *streptanthifolius* (■), var. *borealis* (●), and var. *kluanei* (□).

Figure 4. Holotype of *Senecio streptanthifolius* var. *streptanthifolius*.

Senecio wardii Greene. Pittonia 4:116. 1900. TYPE: "collected somewhere in Utah in the year 1875, by L. F. Ward in the US herbarium labelled *S. aureus* var. *alpinus* Gray." Ward 332 taken to be the type. (HOLOTYPE: US!; ISOTYPE: MO!).

Senecio dileptiifolius Greene. Ottawa Naturalist 15:251. 1902. TYPE: "Mr. Macoun's label for this bears the number 26,679 and indicated that the plant was collected 29 August at an altitude of 6000 feet." Chilliwack Valley, British Columbia. *Macoun 26,679* (HOLOTYPE: NDG!; ISOTYPES: GH! Photos F! CAN!).

Senecio fraternus Piper, Contr. U.S. Nat'l Herb. 11:598. 1906. TYPE: "Mt. Stuart, Kittatas Co., Washington, collected by *Sandberg & Leiberg 553*, July 24, 1893 at an altitude of 1060 m. The type specimen is in the US Nat'l herbarium numbered 285758" (HOLOTYPE: US!; ISOTYPES: F! MO! GH! UC!).

Senecio chapacensis Greene, Leaflets 2:14. 1909. TYPE: "Mt. Chapaca, in Okanogan Co., Washington at 4000′ collected by *A. D. E. Elmer*, August 1897. Collector's n. *592*, as on sheet 352360 US Herb." (HOLOTYPE: US!).

Senecio aquariensis Greenm., Ann. Missouri Bot. Gard. 3:144. 1916. TYPE: "Utah: Aquarius Plateau, at 3050 m., 5 Aug., 1875 *Ward 505*" (HOLOTYPE: MO!; ISOTYPE: GH!).

Senecio malmstenii Blake ex Tidestrom, Proc. Biol. Soc. Wash. 36:183. 1923. TYPE: "Little Podunk Creek, Kane Co., Utah *Malmsten 131*" (HOLOTYPE: US!; ISOTYPES: photo - NY! GH! MO!).

Leaf blades obovate to widely obovate, margins usually entire in the lower 1/2 to 2/3 of the blade, serrate-dentate to crenate near the apex, 2.5–4.0 cm long, (1–)1.3–2.8(–3.5) cm wide; petiole 3–7 cm long; cauline leaves reduced, subentire to lobate. Flowering stalks 2.0–3.5 dm tall. $n = 23, 46$.

DISTRIBUTION. Wooded and open montane areas in northwestern United States, extending north into the interior of British Columbia and south into Utah and Colorado, with a few populations in California.

Senecio streptanthifolius var. *streptanthifolius* exhibits a great degree of morphological variation. In Washington, Oregon and southern British Columbia, var. *streptanthifolius* has obovate leaves with margins usually crenate rather than coarsely dentate. This form is most pronounced in the Wenatchee Mountains of Washington where collections have been identified as *S. suksdorfii* and *S. fraternus*. The collections of J. W. Thompson (#5831, #9502) represent this form well. It can easily be differentiated from var. *wallowensis* by its greater height, larger number of heads and less truncate leaf bases. The specimen of *S. suksdorfii* from OSC cited by Barkley as an isotype has been examined and is clearly representative of this "Wenatchee Mountain" form of var. *streptanthifolius* as are all specimens examined which were collected from the type locality of

S. suksdorfii. It is for this reason that the name *S. suksdorfii* has been reduced to synonymy under var. *streptanthifolius*. The Wallowa Mountain and Mt. Rose Nevada specimens, previously considered part of *suksdorfii,* are united under the new epithet *wallowensis*.

At the southern end of the distribution, the complications resulting from the close relationship between *Senecio neomexicanus* var. *mutabilis* and *S. streptanthifolius* make it difficult to refer many individuals to one group or the other. From limited field studies and extensive herbarium study, I agree with Barkley (1980) that introgression between these taxa (most notably in southeastern Utah but also in southern Colorado) provides a continuum of variation. The results of the phenetic analysis support this inasmuch as *S. neomexicanus* was the only species outside the *S. streptanthifolius* complex to cluster with *S. streptanthifolius*. Flavonoid analysis also reflects a close relationship. *Senecio neomexicanus* var. *mutabilis* could probably be treated as a tomentose variety of *S. streptanthifolius*; however, this would not clarify problems in either *S. streptanthifolius* or *S. neomexicanus*. Because leaf pubescence is relatively useful for characterizing *S. neomexicanus*, var. *mutabilis* is best left as part of *S. neomexicanus*. The type specimen of *S. cognatus* Greene, which Barkley put in synonymy with *S. streptanthifolius* is here removed and placed in synonymy with *S. neomexicanus* var. *mutabilis*. The relationship between *S. oodes* and *S. neomexicanus* is discussed under var. *oodes*.

The relationship of *Senecio tridenticulatus* to *S. streptanthifolius* is not clearly elucidated by this study. Only two collections of *S. tridenticulatus* were made in Colorado where the ranges of the species overlap. *Senecio tridenticulatus* is predominantly a species of the plains and geological parks, so that introgression is only possible in a relatively small portion of its range. Flavonoid profiles were once again too similar to those of *S. streptanthifolius* to be informative. Given that the two have the same chromosome number and that their habitats intergrade, hybridization is to be expected. The type specimen of *S. subcuneatus* Rydb. exhibits *S. tridenticulatus* characters in its leaf shape and may represent just such a hybrid. Confusion arises when trying to separate *S. streptanthifolius* var. *borealis* from *S. tridenticulatus*. Barkley (1978) treated the populations of var. *borealis* from the Great Slave Lake area of Northwest

Territories as disjunct populations of *S. tridenticulatus* where, in fact, they fit very easily into var. *borealis*. They grow in dry, sandy pine stands, are somewhat smaller and have narrower leaves than the more southern Rocky Mountain populations. When these extreme populations are compared to typical *S. streptanthifolius*, they appear out of place but when treated as part of the narrow-leaved var. *borealis*, they fit well.

Senecio pauperculus is also reported to intergrade with var. *streptanthifolius* (Barkley, 1962, 1978). Although flavonoid profiles once again do not aid in elucidating this introgression, morphologically intermediate specimens occur. The evenly crenate-dentate margins of *S. pauperculus* can usually be used to advantage in separating the two taxa. Leathery leaf texture, usually considered a *S. streptanthifolius* character, is also present in *S. pauperculus* populations and so is less reliable. The two species, however, are usually found in different habitats. *Senecio pauperculus* grows in mesic grassy meadows on soil rich in organic matter while *S. streptanthifolius* occurs on rocky sites on sandy well drained soils.

The inclusion of *Senecio malmstenii* in the list of synonymy is certainly provisional; it is an unusual entity which further study may reveal to be unrelated to *S. streptanthifolius*.

REPRESENTATIVE SPECIMENS: **BC.** Chilliwack Valley, *Macoun 26679* (NDG 062991, GH); Mt Apex, SW of Penticton, *Calder & Savile 11715* (RM 256339, UC M290802). **California.** Mono Co: Sonora Pass, Sweetwater Mtns., *Bain 206* (ALTA); Nevada Co: Cisco Trl., Red Mtn., Tahoe NF, *Eggleston 21680* (US 1534313); Shasta Co: Hdwtrs. of Hat Cr., *Eggleston 7494* (NY, GH, US 623893); Sierra Co: Sierraville, *Hall & Babcock 4473* (GH, UC 53868). **Colorado.** Custer Co: Trl. to L. of Clouds, Sangre del Cristo Rg., W of Westcliffe, *Weber 5895* (COLO 61538, MO 1600526); Gunnison Co: N Italian Mtn., *Langenheim 388* (COLO 79378); Huerfano Co: Below Apishapa Pass, *Barkley & Anderson 2448* (NY); Saguasche Co: S of Los Pinos Pass, *Barrell 653 62* (US 2870921). **Idaho.** Bear L. Co: 10 mi W Bloomington, Bear R. Rg., *Baker 9376* (NY); Blaine Co: Boulder Cr. Canyon, Sawtooth NF, *Thompson 14061* (F 946306, MO 1218217, GH, NY, US 1731407); Camas Co: 1 mi W summit, Ketchum, Featherville Rd, Soldier Mtns., *Hitchcock & Muhlick 10421* (NY, CAN 195189, IM 66595, GH, UC 969264). **Idaho.** Cassida Co: Mt Harrison, *Davis 1330* (IM 61707, UC 829725); Clark Co: Spencer L., Dry Cr. Canyon, *Christ 2844* (NY); Custer Co: Lemhi Rg., W Mt. Mogg, *Hitchcock & Muhlick 11232* (GH, US 1923369, IM 66229, CAN 195190, NY, COLO 51932); Franklin Co: Bear R. Rg., 2 mi W Franklin Stn, *Maguire 21638* (IM 104997, NY, UC M249541); Fremont Co: Red Rock Pass, *Christ 5766* (NY); Idaho Co: Heavens Gate, Seven Devils Mtn., *Christ 12520* (NY); Lemhi Co: Gilmore, *Christ & Ward 14846* (NY); Owyhee Co: Three Cr. *Nelson & Macbride 2247* (US 544977, GH); Valley Co: Thunderbolt Mtn., Payette NF, Sawtooth Mtns., *Thompson 13926* (F 946122, IM 59776, US 1727725, GH, MO 1219145, NY). **Montana.** Beaverhead Co: Vipont Park, E

of Sheep Mtn., *Hitchcock & Muhlick 13018* (IM 71241, MO 1295999, UC 757575); Granite Co: Rock Cr. Canyon, Eagle Cr., *Hitchcock & Muhlick 14451* (MO 1302898); Meager Co: 3 mi W Harlowton, on W Sulphur Spgs Rd., *Hitchcock & Muhlick 12069* (IM 70805); Little Belt Pass, *Flodman 910* (US 290955, NY). **Nevada.** Elko Co: 3 mi E of Montello, Utah-Nev. st. line *Train 3748* (NY, IM 53356). **Utah.** Cache Co: Bear R. Range, nr. summit Mt. Magog, *Maguire 14060* (IM 104993, NY); San Pete Co: M. Forks Park, *Maguire 20045* (NY, IM 105035, GH); Salt L. City, *M. E. Jones 1996* (F 252611, US 227883). **Washington.** Chelan Co: Wooded slps. of Mt. Stuart, *Thompson 7641* (ORE, MO 1008888, GH, US 1565200); Mt. Stuart, *Thompson 5831* (MO 991602, GH); Kittatas Co: Beverly Cr. Hd, *Thompson 9502* (NDG 010497, US-G 1419747, MO 1064397, GH, UC 518186; Okanogan Co: near Conconcully-Muckamuck lookout, *Bigelow 116* (MO 1009847, GH); Pierce Co: Iron mtn., Mt. Ranier Nt'l. Pk, *Weigand 2801* (MO 1144349, F 886312); Yakima Co: Mt. Aix, *Thompson 15019* (GH, US 1889126, CAN 195194, MO 1202222, COLO 86185, UC 749564); Mt. Paddo (Mt. Adams), *Suksdorf 73* (GH). **Wyoming.** Lincoln Co: Jacksons Hole, *Payson & Payson 2285* (NY, MO 869176); Teton Co: Taylor Pk., Teton Mtns, *Hall 11455* (UC 217307); SW Wyoming, *Rose 243* (US 48785, RM 68723).

2. **Senecio streptanthifolius** var. **borealis** (T. & G.) J. F. Bain *comb. nov.* BASIONYM: *Senecio aureus* var. *borealis* Torrey and Gray, Fl. N. Am. 2: 442. 1843. *Senecio cymbalariiooides* var. *borealis* (T. & G.) Greenm., Ann. Missouri Bot. Gard. 3: 117. 1916. TYPE: " ', partly Hook.,! *l.c.*" between N.Y. & E.—*Dr.* (presumably Drummond) *s.n.* (LECTOTYPE: GH!). Figures 3 and 5.

Leaf blades oblanceolate to subspatulate, margins entire except for the apex which is dentate usually with 3–7 teeth, cuneate at the base, 1.5–2.5 cm long, 0.8–1.4 cm wide; petiole 2.5–3.5 cm long; cauline leaves usually reduced, entire to subentire and bract-like. Flowering stalks 2.0–3.5 dm tall. $n = 23$.

DISTRIBUTION. Well drained, open, woodland sites in the Rocky Mtns. and the surrounding Boreal Forest region from Yukon and Northwest Territories south to Montana and Wyoming on the eastern side of the Rocky Mountains, while only extending into southern British Columbia on the western side.

The northern populations of *Senecio streptanthifolius*, here segregated as var. *borealis*, all have distinctly oblanceolate leaves with mostly entire margins. Their habitats are fairly uniform as they are most often found on open, sandy or well-drained sites in *Pinus contorta* stands. Typical var. *streptanthifolius* replaces var. *borealis* in southern British Columbia and further east in Montana. However farther east, the southern limit of var. *borealis* extends into

Figure 5. Holotype of *Senecio streptanthifolius* var. *borealis*.

Wyoming where it has been extensively collected in the Bighorn Mountains.

Senecio streptanthifolius var. *borealis* is structurally much less variable than var. *streptanthifolius*. Although *S. streptanthifolius* (*s.l.*) is thought to introgress with two wide ranging species (*S. pauperculus* and *S. canus l.c.* Barkley, 1978) which are sympatric with var. *borealis*, both these species are polyploid within this area of sympatry while var. *borealis* is diploid. Only one collection of tetraploid var. *borealis* was made (*Bain 057*) from central British Columbia. This population was growing within fifty meters of typcial diploid var. *borealis* and typical tetraploid *S. pauperculus*. No convincing evidence of introgression or hybridization between *S. pauperculus* and var. *borealis* was found. After examination of the voucher specimen (M-4754, UC) for the reported hybrid *S. canus* × *S. streptanthifolius* (Ornduff et al., 1967) I feel it is a specimen of *S. canus*. I have found no hybrid specimens of *S. canus* and *S. streptanthifolius* var. *borealis* although I have seen specimens of *S. canus* in the foothills of Alberta that are nearly glabrous.

Senecio streptanthifolius var. *borealis* is separated as a variety because for most of its range it is easily distinguishable from typical *S. streptanthifolius*, although chemically and morphologically the two are similar. Two phytogeographic factors seem to have contributed largely to the differentiation of var. *borealis*. Firstly, var. *borealis* is apparently derived from a relatively small homogeneous portion of the *S. streptanthifolius* complex which was located near the edge of the last glacial advance. Secondly, in its migration into the newly opened territory after glaciation, it was not accompanied by other diploid aureoid species (*S. canus* and *S. pauperculus* are tetraploid or higher in this region) so it was, and remains, relatively free of the introgressive pressures that the southern diploid species exert on one another. Thus it remains distinct from other species of *Senecio* and from var. *streptanthifolius*.

The designation of a lectotype for var. *borealis* was necessitated by Torrey and Gray's failure to typify *Senecio aureus* var. *borealis* in the original description. Torrey and Gray (1843) made two citations in the following order:

> "...*S. aureus*, partly, Hook! l.c.;
> *S. cymbalarioides* Nutt! in Trans. Amer. Phil. Soc. l.c. p. 412..."

From this designation it is clear that Torrey and Gray included *S. cymbalarioides* Nutt. as part of *S. aureus* var. *borealis*, just the opposite of what is proposed here. Without specimens to refer to, however, it is difficult to ascertain the grounds upon which Torrey based their taxon. Greenman (1916) transferred *S. aureus* var. *borealis* to varietal status under *S. cymbalarioides* Nutt. but did not lectotypify the taxon. The first specimen he cited, however, was considered by Greenman to be one of Hooker's collections (at GH) from Arctic America. The specimen was in fact not collected by Hooker but was annotated as having been included in Flora Boreali-Americana. The collector was most likely Drummond as the label bears a distinct "Dr." but no other collector's name (Figure 5). The specimen has been annotated by Torrey and Gray for the Flora of North Amercia (1843) as *S. aureus* var. *borealis*. Conversely, the specimen (at GH) of *S. cymbalarioides* collected by Nuttall from the "Rocky Mountains," bears no annotation label from Torrey and Gray; nor do the Nuttall collections of *S. cymbalarioides* at BM (holotype) or at PH. Thus the Hooker specimen cited by Greenman (at GH) is the only one which can be reliably associated with both the citations given by Torrey and Gray (1843) and with their own description (*l.c.* p. 443). It is therefore chosen as the lectotype for *S. aureus* var. *borealis* T. & G.

REPRESENTATIVE SPECIMENS: **Alberta.** Ft. Chipewyan, *Laing 68* (US 1240083); E side Jasper L., *Morton NA4596* (CAN 359772); 20 mi W of Whitecourt in pine forest, *Bain 173* (ALTA). **BC.** Hwy #7 to Atlin, approx. 40 mi. N of Atlin, *Bain 137* (ALTA); Carson Mtn., Marble Mtns., *Thompson & Thompson 303* (CAN 110452, MO 1233244, UC 749452, F 1481711); 22 mi S of Watson L. open sandy pine forest, *Bain 164* (ALTA); approx. 25 mi W of Dease L. on rd. to Telegraph Cr. in open meadow, *Bain 126* (ALTA); Skagit Valley, *Macoun 69362* (GH, CAN 110456). **Montana.** Jack Cr. Canyon, *Rydberg & Bessey 5266* (NDG 062986, NY, CAN, 195187, F 81934); Midvale, *Umbach 154* (F 191188, US 541500, RM 154897); Carbon Co: Red Rock canyon, Custer NF, *Williams & Williams 3589* (NDG 010487, MO 1123970, GH). **NWT.** McTavish arm, Gt. Bear L., btwn. Labine Pt. & Glacier Bay, *Shacklette 2785* (F 1475875, US 1947342, CAN 200087); mi 19 of Enterprise-Mackenzie R. Hwy., *Thieret & Reich 4875* (US 2344075, CAN 298395); Gt. Slave L., base Maufelly Pt., *Raup 1428* (CAN 311048, GH. **Utah.** Garfield Co: 22 mi N Escalante, along rd. to Bicknell, *Holmgren, Reveal & LaFrance 2516* (BYU 56740, NY, IM 16041). **Wyoming.** Bighorn Co: Ten Sleeps L., *Goodding 414* (F 215583, MO 1719530, US 485236, GH, NY); Johnson Co: Big Horn Mtns. nr. hd. Crazy Woman Cr., *Porter & Porter 9385* (NY, GH, UC M221958); Sheridan Co: S Tongue R. nr. mouth Marcum Cr., *Williams & Williams 3104* (NY, MO 1113205/1109797, GH); Teton Co: Hoback Canyon, *Wehmeyer, Martin & Loveland 5464* (NY, MO 1244197). **Yukon.** Canol Rd., Lo. Ross R., *Porsild & Breitung 9702* (CAN 110459, UC 994746); Whitehorse, E Lewes R., *Porsild & Breitung 9232* (CAN 110460).

3. **Senecio streptanthifolius** var. **kluanei** J. F. Bain *var. nov.* TYPE: Haines Junction, Yukon Territory. *Bain 152* (HOLOTYPE: ALTA). Figures 3 and 6.

A var. *boreali* capitulis magnis paucioribus, foliis basalibus omnino basem includentibus pariter ad marginem dentato-serratis differt.

Herbaceous perennial, 2–3 cm tall, glabrous or occasionally lightly tomentose at the base of the involucres. Stems 1–2, arising from a fibrous rootstock. Basal leaves turgid and leathery, blade obovate to widely oblanceolate, cuneate or narrowly cuneate at the base, margins serrate near the base and serrate or dentate near the apex, 1.5–3.5 cm long, 0.8–1.4 cm wide; petiole 2.5–4.0 cm long; cauline leaves few, entire or subentire to bract-like. Inflorescence a congested, sub-umbelliform cyme of 5–13 heads; involucral bracts 5.0–6.0 mm long. Achenes glabrous. $n = 46$.

DISTRIBUTION. Open disturbed sites in southern Yukon and northern British Columbia.

Senecio streptanthifolius var. *kluanei* is undoubtedly an alloploid species but its origins are somewhat unclear. It has been collected only on disturbed roadsides and as such it appears to be a successional species (i.e., a weed). However this habitat is also occupied by *S. streptanthifolius* var. *borealis*, so it is not a diagnostic feature.

There are obvious morphological affinities with *Senecio pauperculus* including the dentate-serrate lower margins of the basal leaves, disc floret corolla length, disc floret number and involucral bract (phyllary) number. However the flavonoid profile of var. *kluanei* does not indicate any relationship to *S. pauperculus*.

Senecio streptanthifolius var. *kluanei* may also be related to *S. ogoturukensis* Packer, a diploid aureoid senecio inhabiting the same area. The leaf margins of *S. ogoturukensis* are quite variable (Packer, 1972), ranging from entire to deeply serrate to pinnately lobed. The margins of var. *kluanei* fall somewhere between these and the weakly crenate-dentate margins of *S. pauperculus*. Examination of one of the populations of var. *kluanei* revealed a large number of monocephalous individuals which may be construed as evidence of a relationship with *S. ogoturukensis* which also has few heads. However, this relationship is not supported by flavonoid profiles. Although no compounds were identified for *S. ogoturukensis*, examination of two-dimensional chromatograms revealed a

Figure 6. Holotype of *Senecio streptanthifolius* var. *kluanei*.

depauperate profile of between three and four compounds, whereas var. *kluanei* contains ten.

Senecio streptanthifolius var. *kluanei* appears from herbarium specimens to extend into northern British Columbia (*McCabe 704, Rice 55, Raup & Abbe 4163*). One southern population (*Hitchcock & Martin 7409*) collected from south of Savona, British Columbia bears some resemblance; however, the inflorescence is more corymbose and measurement of guard cell lengths revealed cell lengths characteristic of diploid individuals within the *S. streptanthifolius* complex (Bain, 1983, Ph.D. dissertation, University of Alberta, Edmonton). The specimen is thus presumed to be diploid.

REPRESENTATIVE SPECIMENS: **BC.** W & NW slps. of Mt. Selwyn, *Raup & Abbe 4163* (CAN 110454, GH); Taylor Flat, N bank Peace R., *Raup & Abbe 3547* (GH, CAN 110453); Chezacut, *McCabe 704* (UC 542928); Clinton, *Macoun 14779* (CAN 110457). **Yukon.** 1 km E of Haines Jct. on Hwy. #1 (Alaska Hwy.), *Bain 152B* (ALTA); km 1538 Alaska Hwy., W of Whitehorse, *Bain 153* (ALTA); 1 km E of Haines Jct. on Hwy. #1 (Alaska Hwy.), *Bain 152* (ALTA); nr. Stoney Cr., Takhini R., *Michel 26* (US 2050150, GH, UC 674823); 12 E of Champagne, *Michel 21* (US 2050146, GH, UC 674824); L. Labarge, along roadside near campground, *Bain 154* (ALTA); Whitehorse, *Macoun 78961* (F 251955, CAN 153659).

4. **Senecio streptanthifolius** *var.* **rubricaulis** (Greene) J. F. Bain *comb. nov.* BASIONYM: *Senecio rubricaulis* Greene, Pittonia 3:89. 1896. TYPE: "foothills of the Clover Mtns., Nevada, 1893; found by the author" *Greene s.n.* (HOLOTYPE: NDG!). Figures 7 and 8.

Senecio acutidens Rydb., Bull. Torrey Bot. Club 27:180. 1900. Type: "Union Pass, Wyoming. *A. Nelson 858* (type in the herbarium of N.Y. Botanical Garden)" (HOLOTYPE: NY not seen; ISOTYPES: RM! MO! US!).

Senecio jonesii Rydb., Bull. Torrey Bot. Club 27:179. 1900. TYPE: "Utah: Alta, Wasatch Mountains, 1879, *M. E. Jones 1125* (type in Columbia herbarium)" (HOLOTYPE: NY!).

Senecio platylobus Rydb., Bull. Torrey Bot. Club 27:181. 1900. TYPE: "Utah: Wasatch Mtns., 1869, *Watson 671* (type in the Torrey herbarium)" (HOLOTYPE: NY!; ISOTYPES: US! GH!).

Senecio pammelii Greenm., Ann. Missouri Bot. Gard. 3:118. 1916. TYPE: "Utah: moist rocks and shady woods, Peterson Canyon, Peterson, alt. 2895 m., 19 July, 1902 *Pammel and Blackwood 3870* (Mo. Bot. Gard. Herb.)" (HOLOTYPE: MO!).

Senecio rubricaulis var. *aphanactis* Greenm., Ann. Missouri Bot. Gard. 3:174. 1916. *Senecio cymbalarioides* var. *aphanactis* (Greenm.) Blake in Tidestrom, Contr. U.S. Nat'l Herb. 25:614. 1925. TYPE: Utah: dry canyon, Logan, Cache Co., alt. 1525 m., 23 June, 1910 *C. P. Smith 2208* (Field Museum Herb., photograph in Mo. Bot. Gard. Herb.)" (HOLOTYPE: F!; ISOTYPES: UTC, photo-MO not seen).

Figure 7. Holotype of *Senecio streptanthifolius* var. *rubricaulis*.

Leaf blades obovate to ovate, deeply dentate or serrate to lobulate, 2.5–4.5(–7.0) cm long, 1.5–2.8 cm wide; petiole 3–8 cm long; cauline leaves usually lobulate to pinnatifid. Flowering stalks 3.0–4.5 dm tall. $n = 23, 46$.

DISTRIBUTION. Open, dry sites and woodlands, primarily in the mountain ranges of the Great Basin region but also in Colorado and the Sierra Nevada of California.

Senecio streptanthifolius and *S. multilobatus* are sympatric in parts of the Wasatch and Uinta Mountains and adjacent ranges in Utah and Wyoming. On the drier sites, the basal leaves of *S. streptanthifolius* are often more coarsely dentate, even lobate, than are the leaves of typical var. *streptanthifolius*. These populations are all referred to var. *rubricaulis* in this treatment. Barkley (1962) previously referred to this as the *rubricaulis* phase and suggested that it resulted from the introgression of *S. streptanthifolius* and *S. multilobatus*. Morphology supports this idea but flavonoid profiles give no evidence one way or the other (Bain and Denford, 1985). The profiles of all three taxa are similar so no evidence of complementation exists in the *rubricaulis* profile.

Polyploidy has also played a role in adding to the variability in var. *rubricaulis*. The taller, more robust specimens from more mesic sites in the Wasatch Mountains, previously referred to as *Senecio platylobus* (Rydberg, 1900; Greenman, 1916), are apparently tetraploid (Bain, 1985). Flavonoid profiles, however, do not support the separation of this race from the rest of var. *rubricaulis* (Bain and Denford, 1985). Tetraploid populations from more northern locations do not always show the same degree of leaf dissection as do the *platylobus* specimens. These specimens resemble what has been called *S. acutidens* Rydb. in the past. Diploid populations have also been found fitting this description. Their coarsely dentate leaves and taproot appear distinctive when compared with typical var. *streptanthifolius*, but when associated with *rubricaulis* and *platylobus*, the three entities unite in a heterogeneous assemblage.

Separation of the three entities—*acutidens, platylobus*, and *rubricaulis*—into a separate variety, var. *rubricaulis*, is done here based on morphology. A high degree of morphological heterogeneity, relating in part to the two ploidy levels of *rubricaulis*, is still encompassed within the varietal circumscription.

Another problem associated with var. *rubricaulis* is the apparent intergradation of it with *Senecio multilobatus* through a phase of *S. multilobatus* sometimes referred to as *S. uintahensis* (*see* Barkley 1968a). Generally it is possible to separate *rubricaulis* from *uintahensis* based on the consistently more rounded lobes of the basal leaves of *rubricaulis*; however, the two are often similar.

REPRESENTATIVE SPECIMENS: **California.** Mono Co: *Shockley* (F 374230); Lady Bug Pk., *Leiberg 5318* (US 610567). **Colorado.** Eagle Co: Minturu, *Osterhaut 2559* (NY, RM 155045); Garfield Co: near Glenwood Spgs., *Palmer 38121* (MO 1001170, GH); Gunnison Co: Sapinero, *Baker 180* (MO 53295, GH); Jackson Co: Kings Canyon, *Payson & Payson 4288* (MO 932869); Routt Co: Steamboat Spgs., *Goodding 1621* (BYU 193059). **Idaho.** Bannock Co: Pebble Cr., *Cronquist 241–36* (IM 46326); Bannock Co: 11 mi SW of Pocatello, *Christ & Christ 18551* (NY); Bonneville Co: Caribou City, NE slp. of mtn., *Holmgren & Mattala 5459* (BYU 106792, IM 132981, MO 1719798, US 508890, GH); Elmore Co: 4 mi N of Featherville, along Red Warrior Cr., *Baker 10431* (NY); Fremont Co: 14 mi N of Macks Inn below Targhee Pk., *Christ & Christ 19001* (NY); Owyhee Co: Wilson, *Tucker 727* (NY); Power Co: jct. of Bull and Big Canyons, *Foster 6434* (BYU 184711, RM 314726, NY); Teton Co: Victor Mtn. S of town, *Christ 5311* (NY); Twin Falls Co: Shoshone ranger stn., *Gierisch 697* (IM 32948); 25 mi NE of St. Anthony - Big Bend Ridge, *Swisher 22* (COLO 42972). **Nevada.** Elko Co: Copper Mtn., near summit, *Maguire & Holmgren 22337* (US 1924046, IM 56045, GH); Elko Co: W side of Ruby L., *Mason 4659* (UC 566642); White Pine Co: White Pine Mtns., ridge leading E of Currant Mt., *Holmgren, Reveal & LaFrance 2186* (NY); Mountain City, *Nelson & Macbride 2201* (US 544955, MO 712268, IM 55107, RM 75468). **Utah.** Cache Co: Dry Canyon, *Maguire 13829* (IM 33101, US 1785042, GH, RM 186648); Carbon Co: 20 mi N of Wellington, W Tavaplats Plateau, *Maguire 18533* (IM 120072, NY); Daggett Co: Hickerson Park, *Jensen* (IM 62680, GH); Davis Co: Farmington Canyon, above L., *Clark 1449* (IM 133956); Duschesne Co: lo. edge of aspen, Uinta R. Canyon, *Graham 8049* (UC 832054); Garfield Co: E slp. of Mt. Helen - Henry Mtns., *Maguire 19328* (BYU 45941); Kane Co: 15 mi W of Orderville, *Maguire 18803* (BYU 36902, NY, IM 120649, GH, UC M249495); Salt Lake Co: Red Butte Canyon, *Garrett 1854a* (F 246172, GH, RM 56683, NY); Summit Co: near Bear R., *Goodman 1860* (NY, MO 1013596, US 1568139, GH, RM 154903); Uintah Co: Diamond Valley, *Andrews & Noble* (RM 32947); Utah Co: Red Rock Canyon, near Salt L. City, *Rydberg 6064* (US 508562, RM 65817); Weber Co: Mt. Ogden, *Clark 2217* (BYU 112359, IM 135488); Wasatch Mtns., *S. Watson 669* (NY, US 48780, GH). **Wyoming.** Lincoln Co: 15 mi NE of Cokeville, *Cronquist 8811* (NY, IM 101591, UC M249278); Sublette Co: Piney Mtn., 25 mi W of Big Piney, *Meyer & Meyer 2446* (NY, UC 758317, F 1584015, MO 1576244); Teton Co: 6 mi W of Jackson, *Williams 3006* (NY, MO 1113209, GH).

5. **Senecio streptanthifolius** var. **laetiflorus** (Greene) J.F. Bain *comb. nov.* BASIONYM: *Senecio laetiflorus* Greene TYPE: "the type specimens collected by myself in July last, near Boca, California." *Greene s.n.* (HOLOTYPE: NDG!). Figures 8 and 9.

Herbaceous perennial, arising from a fibrous rootstock. Leaf blade ovate to obovate or elliptic, tapering at the base, margins serrulate or crenate to subentire or occasionally deeply dissected, 2.5–7.0(10) cm long, 1.5 3.5 cm wide; petiole (4–)5–9(-11) cm long; cauline leaves few and reduced, lower ones deeply dissected to subentire or bract-like. Inflorescence a loose corymbose cyme of (3–)6–12(–14) heads; involucre glabrous, bracts 4–6 mm long. Achenes glabrous. $n = 23$.

DISTRIBUTION. Open mesic sites in eastern and southern Oregon, adjacent northern California and northwestern Nevada.

Senecio streptanthifolius var. *laetiflorus* is unusual in the *S. streptanthifolius* complex in that its habitat is not predominantly well-drained sites in the boreal or montane forests, but rather the seasonally damp alkali meadows of eastern Oregon and northeastern California. This apparent affinity for more mesic sites allies var. *laetiflorus* with the wide ranging related species *S. pauperculus* and *S. pseudaureus* as well as the more restricted *S. debilis*. *Senecio streptanthifolius* var. *laetiflorus* resembles *S. pauperculus* in a number of structural features including height, cauline leaf dissection and head number, but differs in that its leaves often have entire or subentire margins and a fleshier texture, although not as leathery as in var. *streptanthifolius*. The fact that *S. pseudaureus* in northwestern North America has a chromosome number of $n = 20,40$ indicates that any alliance between it and var. *laetiflorus* is probably superficial.

REPRESENTATIVE SPECIMENS: **California.** Sierra Co: Purdy, *Heller & Kennedy 8665* (F 222285); Sierra Co: 1.5 mi S of Webber L., *Crum 1939* (UC 903106); Siskiyou Co: Gazelle, *Heller 8076* (COLO 86998, UC 128685, F 192280, MO 1719564, US 611174, GH, NY); N California, *Lemmon* (UC 335863); Big valley, *Mrs. Austin 2162* (NY); **Idaho.** Owyhee Co: 1 mi below NY summit, Silver City R., *Baker 8039* (NY); Teton Co: Teton Gorge, Tetonia, *Christ 5452* (NY). **Nevada.** Carson City, *M. Jones* (US 359610); near Carson City, *C. L. Anderson 188* (GH); Washoe Co: Lemmon Valley, *Kennedy 2066* (MO 715497); Washoe Co: Hunters Cr. Canyon *Heller 10479* (UC 176498, F 384806, MO 1719561, US 509761, GH). **Oregon.** Crook Co: *Cronquist 7459* (NY, GH); Grant Co: 4 mi W of John Day, *Peck 19885* (UC 831871, ORE); Harney Co: 4 mi SE of Burns, *Peck 18945* (MO 1285464); Klamath Co: 6 mi N of Ft. Klamath, *Peck 19996* (NY); Klamath Co: Modoc Pt., *Peck 15148* (ORE, NY, MO 949989); Klamath Co: 2 mi N of Keno, *Peck 9393* (NY, MO, GH, ORE); Lake Co: 8 mi W of Lakeview, *Peck 15248* (MO 1042454/949988, NY, ORE); Malheur Co: along Willow Cr. Canyon, *Peck 7115* (ORE); near Devine Ranch, *Leiberg 2411* (F 462209, GH, US 276570, UC 175937, NY); Harney Valley, *Howell* (NY); *Cusick 1617* (F 89471, MO 1719562, US 326141, UC

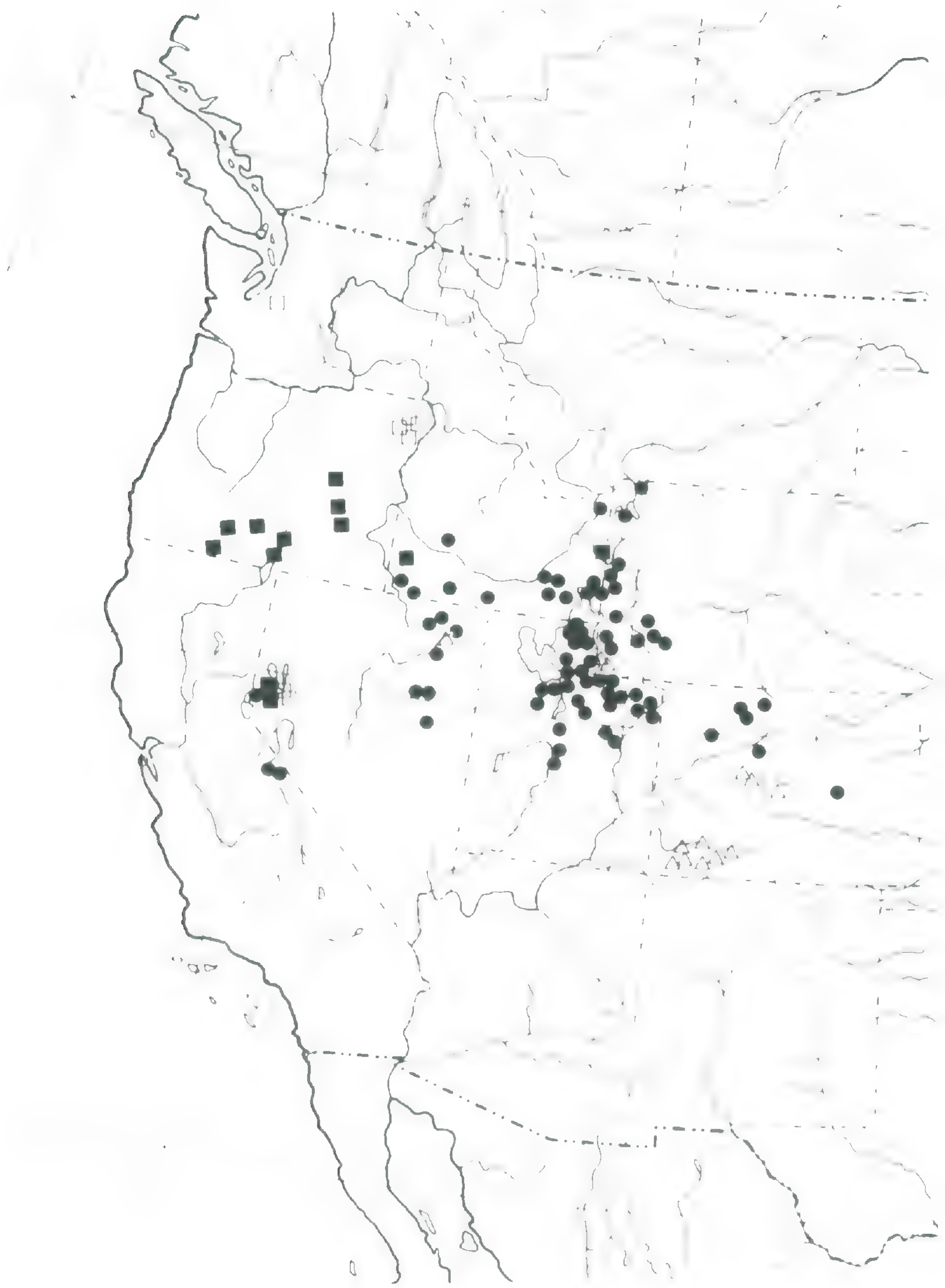


Figure 8. Distribution of *Senecio streptanthifolius* var. *rubricaulis* (●), var. *laetiflorus* (■), var. *wallowensis* (□), and var. *oodes* (Δ).

Figure 9. Holotype of *Senecio streptanthifolius* var. *laetiflorus*.

36035/91326); Annie Cr., *Austin 1618* (US 667469); near Silver L., *Leiberg 764 & 764a* (MO 1719563, GH, US 285752); Otis Cr., *Leiberg 2324* (F 462150, GH, US, 275640, UC 176455, NY).

6. **Senecio streptanthifolius** var. **wallowensis** J. F. Bain *var. nov.* TYPE Ice Lake, Wallowa mountains Oregon. *Bain 199* (HOLOTYPE: ALTA). Figures 8 and 10.

A var. *streptanthifolio* caulibus brevioribus, capitulis magnis paucioribus, basibusque foliorum truncatis usque subcordatis differt.

Herbaceous perennial, 0.9–1.9(–2.5) dm tall, glabrous. Stems 1, or occasionally 2–3 arising from a branching caudex. Basal leaf blade widely ovate or orbicular, obtuse or truncate to weakly cordate at the base, margins serrate or dentate to crenate, 1.1–1.9 cm long, 1.1–1.8 cm wide; petiole 1.5–3.5 cm long; cauline leaves 2–4, bract-like or occasionally dissected. Inflorescence a congested corymbose cyme of 3–7 heads; involucre glabrous, involucral bracts 4.5–5.5 mm long. Achenes glabrous. $n = 23$.

DISTRIBUTION. High alpine and sub-alpine sites in the Wallowa Mtns. in Oregon, Washoe Co. in western Nevada and on Mt. Rainier in the Cascade Mtns.

Senecio streptanthifolius var. *wallowensis* is a small subcaespitose entity which is restricted to open alpine and sub-alpine slopes mostly in western Nevada and eastern Oregon. I define this taxon more narrowly than did Greenman (1912). Greenman referred six collections to *S. suksdorfii* when he published the name change from *S. adamsii* Howell. Of these, only two (*Cusick 3131, Heller 9896*) are var. *wallowensis* according to the present concept. The other four (*Henderson 2309, Suksdorf s.n., Brandegee 915, Tarleton 62*) are var. *streptanthifolius*.

The restricted distribution of var. *wallowensis* may be indicative of the relictual nature of the species. It is known from only three locations in western North America and in no case is it known to occur sympatrically with other species in the complex. It does occur, however, in one instance in the vicinity of another rare aureoid species, *Senecio porteri*. Both species are reported to occur in the Wallowa Mountains. Although var. *wallowensis* has been collected repeatedly over the years in this region, *S. porteri* has apparently been collected only once (*Cusick 2308*, UC! US!). Other than this

Figure 10. Holotype of *Senecio streptanthifolius* var. *wallowensis*.

latter collection, *S. porteri* has been found only in Colorado. The two species are morphologically similar in both having widely ovate leaves with sub-cordate bases; Barkley (1962) described the leaves of *S. porteri* as reniform and both have a disjunct, albeit different distribution pattern. Weber (1965) cited the distribution pattern of *S. porteri* as evidence that it is an Arcto-Tertiary relict. Further study of these two taxa may uncover a link between the alpine aureoid senecios (*cf.* Packer, 1972) and the *S. streptanthifolius* complex. The close relationship between var. *wallowensis* and var. *laetiflorus* has been previously discussed.

REPRESENTATIVE SPECIMENS: **Nevada.** Washoe Co: near Mt. Rose, *Howell 14176* (MO 1151297); E of Mt. Rose on Jones Cr. trail, *Train 4393* (NY, IM 93619, UC 831974); Mt. Rose *Heller 9896* (F 251942); Big Meadows, *Williams, Howell, Tiehru, Gez, Lott 78-248-7* (IM 160777). **Oregon.** Wallowa Co: steep slps. of Matterhorn, Wallowa Mtns., *G. Mason 1760* (ORE); Wallowa Co: Ice L., *Peck 18502* (ORE); Ice L., Wallowa Mtns., *Bain 199* (ALTA); high slp. above Jewitt L., Wallowa Mt., *Peck 18055* (ORE); near summit Pete's Peak, *Peck 17943* (UC 832102); Ice L., *Ownbey & Ownbey 1842* (F 1607597, US 1789882, MO 1211791, GH, RM 183640); Ice L. Wallowa Mt., *Peck 18514* (ORE, NY); steep mtn. sides of Imnaha R., *Cusick 3131* (F 225018, MO 1719799, GH, NY); Pete's Pt., *G. Mason 1371* (ORE); Peets Pt., Wallowa Mtn., *Peck 17961* (ORE). **Washington.** Pierce Co: Iron Mtn., Mt. Rainier NP, *Flett 3246* (MO 851663).

7. **Senecio streptanthifolius** var. **oodes** (Rydberg) J. F. Bain *comb. nov.* BASIONYM: *Senecio oodes* Rydb. Bull. Torrey Bot. Club 33:158. 1906. TYPE: "Colorado Mtns. Harvard. 1896, *F. E. Clements 39* (type)" (HOLOTYPE: NY!). Figures 8 and 11.

Senecio leonardii Rydb. Bull. Torrey Bot. Club 37: 468. 1910. TYPE: "Utah: near divide, head of American Fork Canyon, July 29, 1885. *Leonard 143* (type in herbarium of N.Y. Botanical Garden)" (HOLOTYPE: NY!).

Herbaceous perennial, loosely floccose-tomentose especially in the leaf axils and at the bases of the involucres. Basal leaves floccose-tomentose, occasionally glabrate with age, blade obovate to ovate or occasionally widely ovate, cuneate or sometimes obtuse at the base, margins evenly serrate to crenate, 3–4 cm long, 1.5–2.7 cm wide; petiole stout, 2.5–7(–9) cm long; cauline leaves few, reduced upward, the lower ones resembling the basal leaves but often more oblanceolate and more dissected, the upper ones usually greatly reduced and entire. Inflorescence a corymbose cyme of 6–13 woolly heads; involucre often dark in color; involucral bracts 4–5.5 mm long, tomentose at least at the base. Achenes glabrous. $n = 23$.

Figure 11. Holotype of *Senecio streptanthifolius* var. *oodes*.

DISTRIBUTION. Disturbed open sites at higher elevations in southwestern and central Colorado (Lake, Eagle, and Summit counties); also Wyoming and neighboring Utah as well as Elko Co., Nevada.

Senecio streptanthifolius var. *oodes* includes both the *leonardi* phase and the *molinarius* phase as outlined by Barkley in 1962. In his 1978 treatment, Barkley placed *S. molinarius* in synonymy with *S. wernaerifolius* where it belongs judging from the type specimen (GH). However, Barkley's clear designation of the Bethel, Willey, Clokey specimen (#4391) as representative, leaves little doubt about what he envisioned as the *molinarius* phase; he separated the two phases largely on the amount of pubescence present. The two phases were judged sufficiently similar in this study to warrant their being combined as the *leonardi* phase. Subsequent structural, chemical and chromosomal analyses all support the merging of these taxa. Examination of the type of *S. oodes* Rydb. revealed it to be part of this taxon; since *S. oodes* predates *S. leonardi,* it is the legitimate name at the species level. The appropriate new varietal combination is made here. As with other aureoid taxa, var. *oodes* embodies some degree of variation so it is perhaps unfortunate that the type specimen of *S. oodes* is less distinctive than that of *S. leonardi.* The loosely floccose, thick leaves with crenate margins are visible on the type specimens of both *S. oodes* and *S. leonardi,* as are the basally slightly villous to floccose involucres. The variation in the amount of the tomentum present on the leaves of var. *oodes* makes the examination of the other characters necessary for accurate identification. Even so, difficulty sometimes arises in separating *S. neomexicanus* var. *mutabilis* from var. *oodes* in southwestern Colorado (*see* Barkley, 1968b). *S. streptanthifolius* var. *oodes* has generally wider leaves with a smaller leaf/petiole length ratio and more regularly toothed margins. In addition, Greenman separated the two taxa (*S. leonardi* and *S. mutabilis sensu* Greenman) on the basis of var. *oodes* having glabrous achenes (a trait also ascribed to *S. oodes* by Rydberg) while *S. mutabilis* has hirtellous achenes. Achene pubescence is not presented here as a useful distinguishing character. Flavonoid profiles clearly separate var. *oodes* from *mutabilis*, while the shared presence of isorhamnetin 3/7 glycosides between *S. canus* and var. *oodes* suggests that var. *oodes* may be more closely related to *S. canus* than it is to *S. neomexicanus* var. *mutabilis.*

REPRESENTATIVE SPECIMENS: **Colorado.** San Juan Mtns., E side Wolf Cr. Pass, *Hall 11107* (UC 217254); near Breckinridge, Mt. Guyot, *Anderson* (MO 718571); Durango, *C. S. Crandell 3048* (NY); 7 mi W of Placerville, *Kelly 1529* (COLO 57298); Archuleta Co: Pagosa Spgs., *Bethel, Willey, Clokey 4391* (F 515570, MO 880556, US 1113895, UC 831966, NDG 010491); Eagle Co: Red Cliff, *Osterhaut 2703* (COLO 321801, NY); Gunnison Co: Parlius, *Eastwood* (COLO); Hinsdale Co: Lake City, *Ramaley 16489* (COLO 11265); Laplata & San Juan Co: Silverton, *Michener 325* (COLO 167870); Lake Co: *Mosquin & Gillett 5363* (UC M287578); Mineral Co: 5 mi below Wolf Cr. Pass on Hwy. 160, *Anderson & Barkley 2523* (NY); Rio Grande Co: E side of Wolf Cr Pass on roadside, *Bain 096 & 096a* (ALTA); Summit Co: near Breckinridge, *Mackenzie 154* (MO 2966997). **Nevada.** Elko Co: E Humboldt Mtns., *Watson 668* (GH, US 48778). **Wyoming.** Huerfano Co: 2 mi below Apishapa Pass, *Barkley & Anderson 2451* (NY, MO 2500338); Uinta Co: near Bear R., *Payson & Payson 4822* (US 1439689, MO 974495/974496, GH, RM 115231).

ACKNOWLEDGMENTS

The author thanks K. E. Denford, J. G. Packer and S. J. Wolf for helpful advice; J. McNeill and P. Eckel for providing Latin diagnoses; T. M. Barkley for much helpful advice and a careful review of an earlier version of the manuscript; and Joann Creager for much field and editorial assistance.

Financial support from the Boreal Institute for Northern Studies (to J. F. B.) and NSERC Canada (to K. E. Denford and J. F. B.) is also gratefully acknowledged.

LITERATURE CITED

BAIN, J. F. 1985. Chromosome numbers in the aureoid *Senecio* complex (Asteraceae). Canad. J. Bot. 63:539–542.

_____, AND K. E. DENFORD. 1985. Flavonoid variation in the *Senecio streptanthifolius* complex. Canad. J. Bot. 63:1685–1690.

BARKLEY, T. M. 1962. A revision of *Senecio aureus* and allied species. Trans. Kansas Acad. Sci. 65:318–408.

_____. 1968a. Taxonomy of *Senecio multilobatus* and its allies. Brittonia 20:267–284.

_____. 1968b. Intergradation of *Senecio* sections *Aurei, Tomentosi*, and *Lobati* through *Senecio mutabilis* Greenm. (Compositae). Southw. Naturalist 13: 109–115.

_____. 1978. *Senecio*. pp. 50–139. *In*: C. T. Rogerson, Ed. N. Amer. Flora series II pt. 10. New York Bot. Gard.

_____. 1980. Taxonomic notes on *Senecio tomentosus* and its allies (Asteraceae). Brittonia 32:291–308.

_____. 1988. Variation among the aureoid Senecios of North America: a geohistorical interpretation. Bot. Rev. 54: 82–106.

BILLINGS, W. D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. Ecology 31:62–74.

_____. 1977. Alpine phytogeography across the Great Basin. Great Basin Naturalist 2:105–117.

CARMICHAEL, J. W. 1980. The TAXMAP classification program. Univ. of Alberta Computing Services [pamphlet] 0104.0280 13p.

_____ and P. H. A. Sneath. 1969. Taxometric maps. Syst. Zoo. 18:402–415.

GREENMAN, J. M. 1912. Some plants of western America. Bot. Gaz. (Crawfordsville). 53:510–512.

_____. 1916. Monograph of the north and central American species of the genus *Senecio*, Part I. Ann. Missouri Bot. Gard. 3:85–164.

HULTÉN, E. 1937. Outline of the History of the Arctic and Boreal Biota During the Quaternary Period. Bokforlags Akiebolaget Thule., Stockholm.

KOWAL, R. R. 1975. Systematics of *Senecio aureus* and allied species on the Gaspé Peninsula, Quebec. Mem. Torrey Bot. Club 23:1–113.

MATTHEWS, J. V. 1979. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. pp. 34–86. *In*: H.V. Danks, Ed., Canada and Its Insect Fauna. Mem. Entomol. Soc. Canad. No. 108.

MORTON, J. K. 1981. Chromosome numbers in Compositae from Canada and the U.S.A. J. Linn. Soc., (Bot.) 82:357–368.

ORNDUFF, R., T. MOSQUIN, D. H. KYHOS AND P. H. RAVEN. 1967. Chromosome numbers in Compositae VI. Senecioneae II. Amer. J. Bot. 54:205–213.

PACKER, J. G. 1972. A taxonomic and phytogeographical review of some arctic and alpine *Senecio* species. Canad. J. Bot. 50:507–518.

RYDBERG, P. A. 1900. Studies of the Rocky Mountain flora I. Bull. Torrey Bot. Club 27:169–189.

SCHISHKIN, B. K. 1961. *In*: V. L. Komarov, Ed., Flora Urss, Vol. XXVI. Institution botanicum nominae Academiae Scientiarum, USSR.

STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia University Press, New York.

TORREY, J. D. and A. GRAY. 1843. A Flora of North America, Vol. 2. Hafner Publishing Co., New York.

TUTIN, T. G., V. H. HEYWOOD, N. A. BURGES, D. M. MOORE, D. H. VALENTINE AND S. M. WALTERS. 1976. Flora Europea Vol. 4. Cambridge Press, Cambridge.

WEBER, W. A. 1965. Plant geography in the southern Rocky Mountains. pp. 453-468. *In*: H. E. Wright and D. G. Frey, Eds. The Quaternary of the United States. Princeton University Press.

WOLFE, J. A. 1978. A paleobotanical interpretation of tertiary climates in the northern hemisphere. Amer. Sci. 66:694–703.

DEPARTMENT OF PLANT SCIENCE
MACDONALD COLLEGE
STE. ANNE DE BELLEVUE, QUEBEC H9X 1C0
CANADA

RHODORA, Vol. 90, No. 863, 1988

A REEVALUATION OF THE *TRIGLOCHIN MARITIMUM* COMPLEX (JUNCAGINACEAE) IN EASTERN AND CENTRAL NORTH AMERICA AND EUROPE

BRUCE A. FORD AND PETER W. BALL

ABSTRACT

Triglochin maritimum L. is a circumboreal aggregate species complex comprised of a number of different cytotypes. Numerical analyses of morphological variation in plants from eastern and central North America and Europe indicate that two species, *T. maritimum* and *T. gaspense* Lieth & Löve, can be recognized. *Triglochin maritimum* is a polymorphic species, of wide distribution that is characterized by densely flowered racemes, erect leaves that are shorter than the scape, and by its long stigmatic papillae. *Triglochin gaspense*, restricted to coastal marshes of the Maritime Provinces and the State of Maine, is distinguished by its lax racemes, arcuate leaves that are longer than the scape and its short stigmatic papillae. Differences in habitat preference lend further support to this classification.

Key words: *Triglochin*, Juncaginaceae, taxonomy, North America, Europe

INTRODUCTION

Triglochin maritimum L. is a circumboreal aggregate species comprised of cytotypes ranging from $2n = 12$ to $2n = 144$ (Löve and Löve, 1958). Morphological variability, wide distribution and polyploidy have resulted in a varied taxonomy that is well reflected in the literature (*see* Taxonomic History). Cytological and morphological variability appear to be particularly high in eastern and central North America and Europe, where a number of different cytotypes have been described (Löve and Löve, 1958; Dandy, 1980). Löve and Löve (1958) and Love and Lieth (1961) proposed the specific recognition of many of these cytotypes. These taxa, distinguished primarily on the basis of chromosome number and on minor differences in morphology, were treated as: *T. debile* (Jones) Löve & Löve ($2n = 96$) from the North American midwest; *T. elatum* Nutt. ($2n = 144$) from eastern North America; *T. maritimum* ($2n = 48$, but also 12,24,30,36) from Europe and perhaps the east coast of North America; *T. gaspense* Lieth & Löve ($2n = 96$) from Atlantic North America and *T. concinnum* Davy from the west coast of North America. These two treatments relied on a few poorly defined characters to delimit taxa and were therefore largely inconclusive.

In the present study, morphological variation was analyzed in specimens from eastern and central North America and Europe. Our main objective was to determine trends of morphological diversity, and in conjunction with ecology and geographic distribution, to produce a classification that reflects differences amongst the various taxa.

TAXONOMIC HISTORY

Linnaeus (1753) originally described *Triglochin maritimum* L. from Sweden. Although several cytotypes are known from Europe, they have not been given formal taxonomic recognition (c.f. Löve and Löve, 1958; Dandy, 1980).

In North America, however, polyploidy in conjunction with variation in ligule shape and length, leaf shape and angle, pollen grain diameter, spacing of flowers on the raceme, and general stature of the plants has resulted in a proliferation of names.

Triglochin concinnum Davy ($2n = 48$) was originally described from the salt marshes of San Francisco Bay by Davy (1895) and was said to differ from *T. maritimum* in having terete leaves and bilobed ligules. Subsequent studies by Howell (1947) and by Löve and Löve (1958) supported Davy's circumscription, and most recent floras of western North America recognize this taxon (Munz, 1963; Mason, 1957; Hultén, 1962; Hitchcock et al., 1971). Scoggan (1978), however, placed it in synonymy under *T. maritimum*.

Triglochin debile (Jones) Löve & Löve was first described from Utah as *T. maritimum* L. var. *debile* by Jones (1895). Howell (1947), feeling that its affinities were with *T. concinnum*, transferred it to that species. However, Löve and Löve (1958), noting differences in chromosome number, elevated it to specific rank. Most recent taxonomic works have largely ignored the Löves' taxonomy, either disregarding the taxon (Looman, 1976; Scoggan, 1978; Moss, 1983), accepting Jones's original classification (Hultén, 1962), or regarding it as a variety of *T. concinnum* (Hitchcock et al., 1971; Van Bruggen, 1976; Kaul, 1986).

Nuttall (1818) described *Triglochin elatum* Nutt. from New York State, distinguishing it from *T. maritimum* L. on the basis of fruit characteristics. This name was later reduced to a variety of *T. maritimum* by Gray (1856), to synonymy by Watson and Coulter (in Gray, 1889), and is not even mentioned by Fernald (1950) and Gleason (1952). Löve and Löve (1958), however, noting a chromosome number of $2n = 144$ for plants in Québec, proposed that Nuttall's

name be reinstated and applied to all plants in eastern North America. While some manuals have used the name *T. elatum* Nutt. either at the specific level (Erskine, 1960; Roland and Smith, 1969) or at the varietal level (Kaul, 1986), most taxonomic treatments (Seymour, 1969; Hitchcock et al., 1971; Voss, 1972; Rousseau, 1974; Scoggan, 1978; Crow and Hellquist, 1982; Hinds, 1986) have simply referred to these plants as *T. maritimum*.

Fernald (1903) was the first to describe a dwarf form of *Triglochin maritimum* L. from northeastern North America. This form was found to occur in areas below the high water mark where daily tidal fluctuations were thought to contribute to its small stature. Fernald did not give this plant taxonomic recognition as he considered it but a phenotypic variant. Fernald (1950) made further reference to this plant when he stated that "the smallest diffuse individuals with open racemes are *T. concinna* Davy, hardly a distinct species." The name *T. gaspense* Lieth & Löve was published by Löve and Lieth (1961) who cited morphological, cytological, geographical and ecological differences between this plant and other members of the *T. maritimum* L. complex. Most works published since that time (Catling et al., 1985; Crow and Hellquist, 1982; Hinds 1983, 1986; Seymour, 1969) have recognized this taxon, although Rouleau (1978) referred to it as a hybrid between *T. maritimum* L. and the tri-carpellate species *T. palustre* L.

METHODS

The preliminary part of this investigation consisted of an herbarium study of specimens of the *Triglochin maritimum* complex from eastern and central North America and Europe. In all, approximately 1000 specimens were examined from CAN, DAO, MT, TRT and TRTE (herbarium abbreviation according to Holmgren et al. 1981) and from collections made in New Brunswick and the Gaspé in 1984 and 1986. We discovered that most specimens could not be assigned to a particular taxon using traditional morphological characters and had to be categorized on the basis of their geography. The only exceptions to this rule were specimens of *T. gaspense* Lieth & Löve, which could be classified on the basis of small stature and leaves exceeding the scape.

The numerical analysis of morphological characters was based on 274 specimens, 138 in flower and 136 in fruit. These two groups were treated as separate data sets because of the difficulty in finding fruit

and flower on the same specimen. Specimens were chosen to reflect the apparent geographic range of each taxon and included paratypes of *Triglochin gaspense* Lieth & Löve and specimens determined by D. and A. Löve and H. Lieth. Fifty operational taxonomic units (OTUs) were selected for each taxon, 25 in fruit and 25 in flower. The groups used in this study were defined as: *T. debile*, *T. elatum* (inland) (plants from fresh water wetlands in northeastern North America), *T. elatum* (coastal) (plants from the salt marshes of northeastern North America), *T. gaspense* and *T. maritimum* (European plants). There was inadequate material of *T. concinnum* available for study. In addition, 24 specimens (13 in flower and 11 in fruit) from St. Omer, Québec, representing all the individuals from a transect through a mixed population of *T. gaspense* and *T. elatum* (coastal), were included in the data sets. A total of 11 characters was used in the study, 9 in flower (scape height, scape width, raceme density, leaf angle, tepal length, stamen length, pollen diameter, stigma papillae length, leaf length in relation to scape height), and 7 in fruit (scape height, scape width, raceme density, leaf angle, carpel length, seed length, leaf length in relation to scape height). Each specimen was scored for the appropriate compliment of characters, and from these data a variety of matrices were formed. A list of the specimens used in the numerical analyses as well as summary statistics are available from the senior author upon request.

The multivariate numerical analyses were carried out in three stages. The first stage involved the selection of 10 OTUs of each taxon, with pollen sizes similar to those described by Löve and Lieth (1961). Since these authors found pollen diameter to best differentiate taxa and since pollen size can reflect ploidy, OTUs were selected on the basis of this character in addition to geography in an attempt to separate groups and locate character discontinuities. Secondly, multivariate analyses were carried out among all OTUs in fruit and flower to determine overall phenetic patterns and groups that may be present. Thirdly, to eliminate the influence of one group on another, a series of pairwise comparisons of taxa were undertaken.

Principal components analysis (PCA) and cluster analysis, using the unweighted pair-group method of averaging (UPGMA), were performed using the NTSYS package of numerical techniques (Rohlf et al., 1982). The data used in these analyses were standardized to zero mean and unit variance to eliminate the gross size factor and provide equal weighting to each variable.

PCA was used to determine overall variation in the data sets and was accomplished employing the standard *R*-technique using Pearson correlation coefficients and unweighted principal components. Cluster analysis was performed on dissimilarity matrices based on average taxonomic distance measurements. Phenograms were prepared using UPGMA because it was found to give the highest cophenetic correlation and thus the least amount of distortion of the original matrix in comparison to other clustering methods.

To achieve the greatest separation or discrimination of taxa and to test the significance of the groups, a discriminant functions analysis (DFA) using the BMDP7M program (Dixon 1983) was employed. Variables are entered into the discriminant function in a stepwise manner, on the basis of the highest residual *F*-value, until maximal separation of the predetermined groups is achieved. Canonical variates were then used to represent the discriminant space. OTUs from St. Omer were not used in the discriminant function but were assigned to groups on the basis of the classification of the other five taxa.

All variables were included in the PCA and cluster analyses. The leaf/scape variable was excluded from the DFA to avoid the circularity of basing some groups on this character and subsequent discrimination based upon this same variable.

RESULTS

Taxonomic characters

A review of the morphological differences between members of the *Triglochin maritimum* complex was given by Löve and Lieth (1961). It is not the intent of this paper to repeat their review, but rather to consider in some detail those characters that separate taxa and to discuss discrepancies between the two studies.

1. SCAPE HEIGHT. Scape height was an inconsistent character and was of no use in distinguishing members of the *Triglochin maritimum* complex. While *T. gaspense* has shorter scapes on average (144.9 ± 34.2 mm fruiting, 114.16 ± 44.2 mm flowering) than any of the other taxa, there was considerable overlap in the range of this character in all groups examined.

2. SCAPE WIDTH. Scape width narrows towards the apex of the plants examined and for this reason all measurements were taken immediately below the raceme. Like scape height, scape width is a

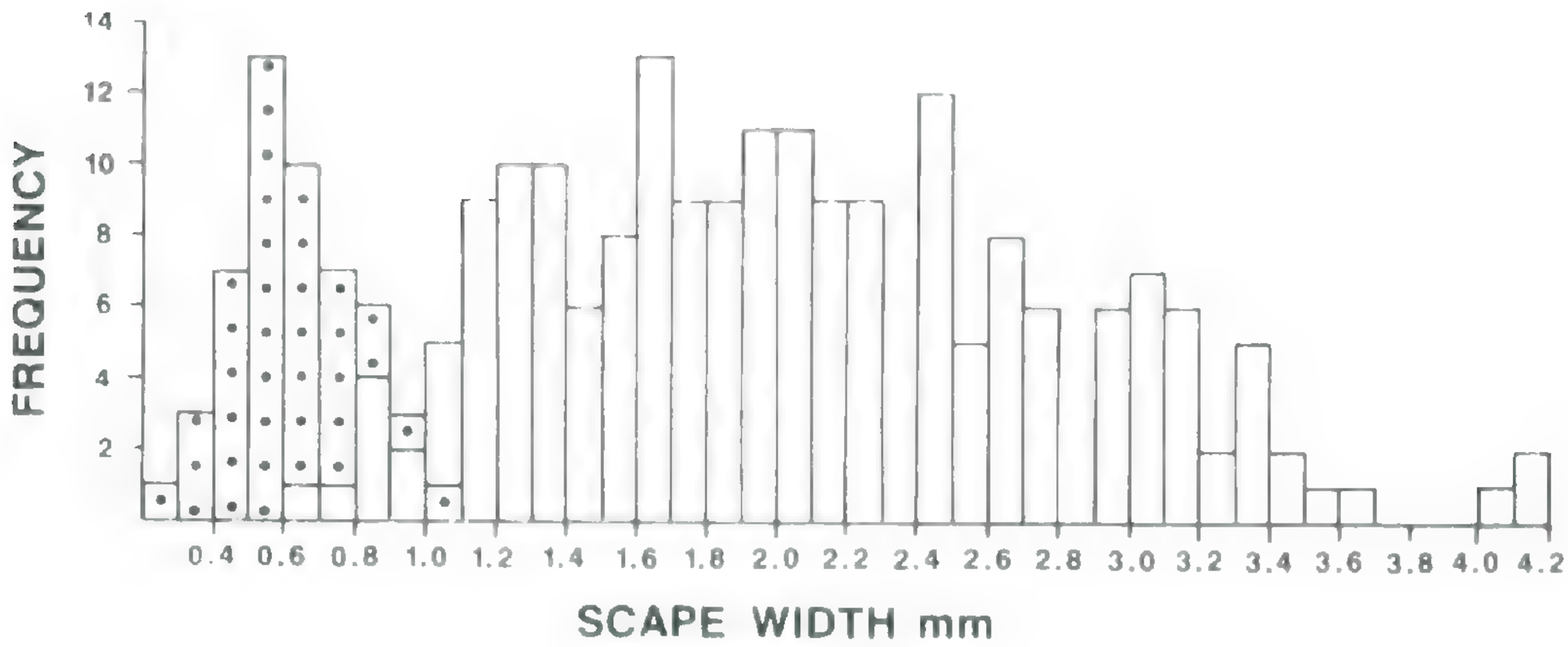


Figure 1. Frequency diagram of scape widths in *Triglochin gaspense* ⊡ and the non-*gaspense* taxa □, for all flowering and fruiting specimens examined (n = 250).

variable character and was of no use in distinguishing among *Triglochin elatum* (inland), *T. elatum* (coastal), *T. debile*, and *T. maritimum*. On the other hand, *T. gaspense* had narrower scapes (0.7 ± 0.2 mm fruiting, 0.6 ± 0.2 mm flowering) than other members of the complex. Although there is an overlap in the ranges of all taxa, the frequency with which it occurs in *T. gaspense* is quite low (Figure 1). Only 8 out of 200 non-*gaspense* OTUs were found to have scapes < 1.0 mm; conversely, only one *T. gaspense* specimen was found to have a scape > 1.0 mm. In most instances, therefore, scape width provided a good separation of *T. gaspense* from the rest of the *T. maritimum* complex.

3. Leaf/Scape relationship. The scape heights found in the *Triglochin maritimum* complex ranged from those that extended beyond the leaves to those that were considerably shorter than the leaves. Because of leaf breakage in herbarium specimens it was not possible to precisely quantify the leaf/scape relationship, but it was possible to assign each OTU to one of the following categories:

1. Top of the scape exceeding the leaf tips by more than 25%.
2. Top of the scape 10 to 24% higher than the leaf tips.
3. Top of the scape equal to the leaf tips.
4. Top of the scape 10 to 24% shorter than the leaf tips.
5. Top of the scape shorter than the leaf tips by more than 25%.

Leaf length in relation to the height of the scape provided a character that gave almost complete separation of *Triglochin gaspense* from the other taxa, but failed to provide any distinction between the other taxa. The non-*gaspense* taxa had scores from 1–3 (only one specimen had a score of 5), while *T. gaspense* was characterized by scores of 3–5.

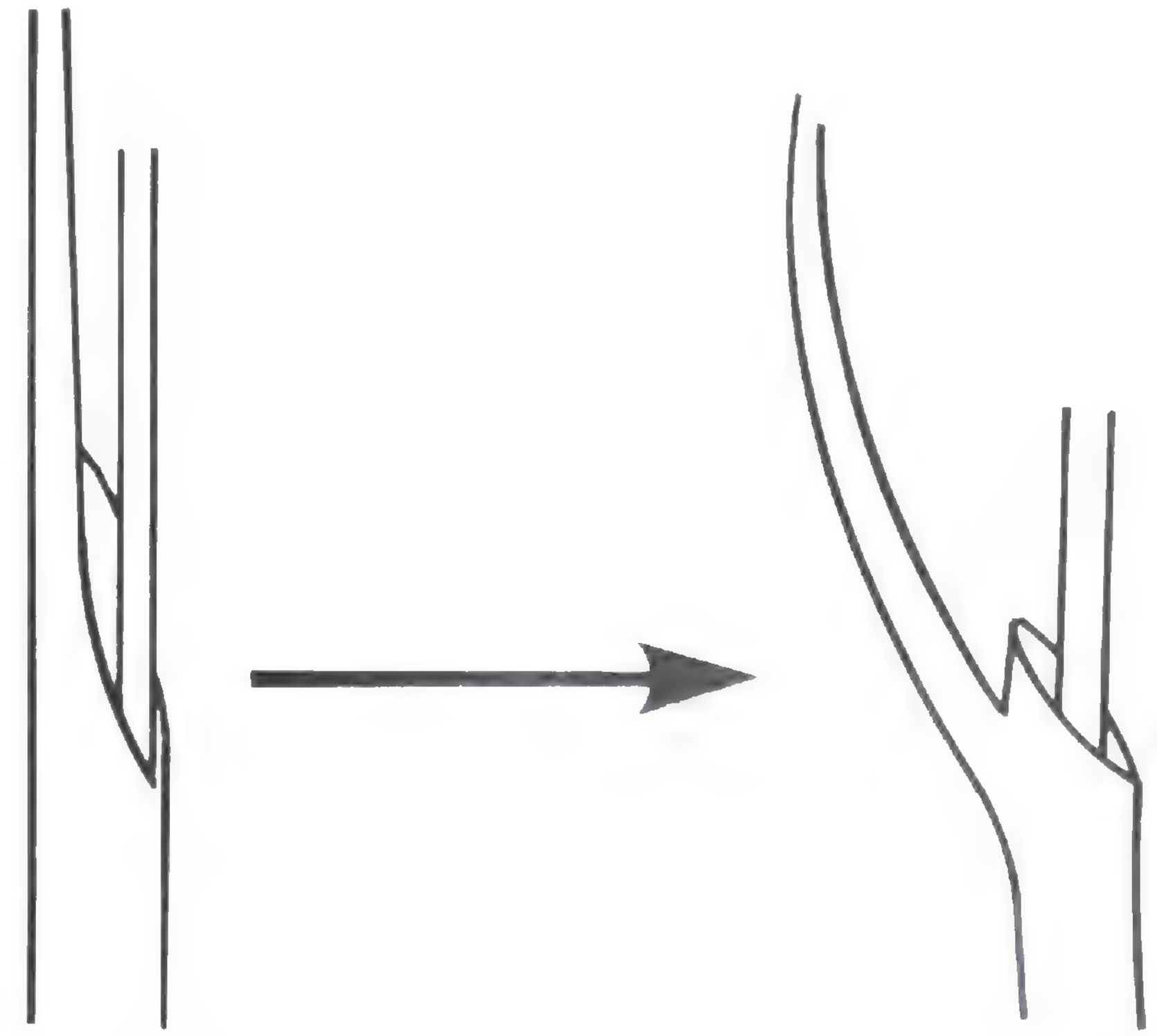


Figure 2. Extremes of leaf angles found in members of the *Triglochin maritimum* complex.

4. Leaf angle. Members of the *Triglochin maritimum* complex possessed leaf blades that ranged from erect and straight to patent and arcuate (Figures 2 and 3). Some degree of leaf curvature was evident in three taxa (*T. elatum* (coastal), *T. maritimum*, and *T. gaspense*); however, the frequency with which that condition occurred in the first two taxa was relatively low (4 and 7 out of 50 OTUs respectively). On the other hand, *T. gaspense* was found to have patent, arcuate leaves in 46 out of the 50 OTUs examined. The degree of leaf curvature was highly variable in this taxon but appeared to be present in nearly all specimens (Figure 3). Leaf curvature is easily seen on live plants, but because of the compression and distortion of leaf blades that occurs during preparation of dried specimens, it can be difficult to detect on some herbarium material. However, most herbarium sheets held several plants, and arcuate leaves were usually evident on at least some of them.

The high frequency of leaf curvature in *Triglochin gaspense* could be regarded as a phenotypic response to frequent tidal disturbances. However, two lines of evidence suggest that this character may have some genetic basis. First, *T. concinnum*, which grows in a similar

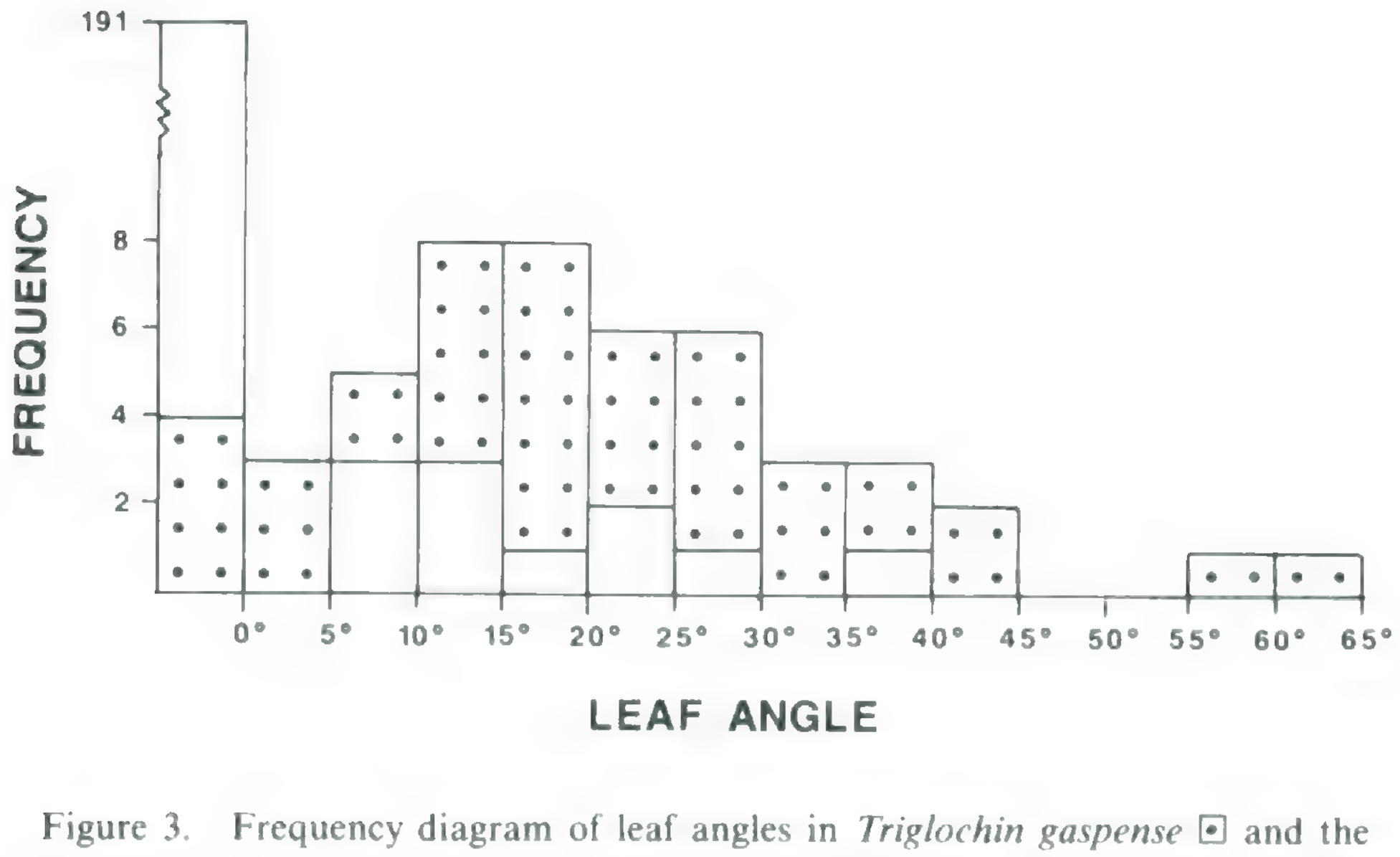


Figure 3. Frequency diagram of leaf angles in *Triglochin gaspense* ⊡ and the non-*gaspense* taxa □, for all flowering and fruiting specimens examined (n = 250).

habitat to *T. gaspense*, fails to exhibit this character. Second, plants transplanted to controlled conditions in the glasshouse, without being submitted to inundation or to high salinity, still maintained their curved leaves.

5. Ligules. Although ligule morphology has been used by some authors (Löve and Lieth, 1961; Howell, 1947; Hitchcock et al., 1971; Munz, 1963; Kaul, 1986) to distinguish between members of the *Triglochin maritimum* complex, it could not be consistently employed in this study because of the difficulty of observing this character without damage to herbarium material.

In their description of morphological characters, Löve and Lieth (1961) stated that:

> "the ligule in the dwarf plants (*T. gaspense*) is short, 1/2 to barely 1 mm long, and sometimes slightly hood shaped. In *T. concinnum*, the ligule is likewise cucullate and often attached at the middle, giving the impression of being bilobed. In *T. debile* the ligule is slightly longer than our small form, often 2 mm long, hood shaped or square, but in *T. elatum* it is always very long, 4–5 mm, and acute."

In the descriptions and keys used by the other authors listed above, both *Triglochin concinnum* and *T. debile* were distinguished from *T. maritimum sensu lato* by their bilobed ligules.

Table 1. Comparison of ligule lengths (mm) from population samples of members of the *Triglochin maritimum* complex (n = number of plants).

Locality	Mean	SD	Range
T. elatum (inland), Chief Point Bay, Ont. (n = 10)	1.0	0.3	0.7–1.4
T. elatum(coastal), La Grande-Mare, P. Q. (n = 10)	1.5	0.5	1.0–2.5
T. elatum (coastal), Pointe-au-Père P. Q. (n = 13)	1.8	0.4	1.1–2.6
T. gaspense, Douglas Town, P. Q. (n = 15)	0.5	0.2	0.3–1.0
T. gaspense, St. Omer, P. Q. (n = 10)	0.8	0.2	0.6–1.1
T. gaspense, Pokesudie Island, N. B. (n = 16)	1.1	0.1	0.9–1.5

Table 1 shows the range of variation found in ligules measured on population samples from Chiefs Point Bay, Ont. (*Bezdeck 4679*, TRTE), (*Triglochin elatum* inland), Pointe-au-Père (*Ford & Ford 86138*, TRTE), and La Grande Mare, P.Q. (*Ford & Ford 86200*, TRTE) (*T. elatum* coastal), Douglas Town (*Ford & Ford 86201, TRTE) and St. Omer, P.Q. (Ford & Ford 86168*, TRTE) and Pokesudie Island, N.B. (*Ball 84233* TRTE), (*T. gaspense*). The long, acute ligules "characteristic" of *T. elatum* were not seen in any of the populations sampled, but ranged from 0.7 mm in plants from Chiefs Point Bay to 2.6 mm in the Pointe-au-Père population. Ligule lengths from 0.6 mm to 1.5 mm were evident in specimens of *T. gaspense* from St. Omer and Pokesudie Island respectively, and shapes appeared to span a continuum from cucullate to semi-circular. Bilobed ligules are supposedly characteristic of *T. debile*. In those specimens of *T. debile* where it was possible to observe ligules, they were often only entire, or both bilobed and entire ligules could be found on the same plant. Despite the limited number of plants examined, there is evidence to suggest that ligule shape and length can be misleading characters that are of questionable taxonomic use.

6. Leaf bases. Evanescent, fibrous leaf bases, in contrast to those that persist for several seasons have been used to distinguish *Triglochin gaspense* from other members of the *T. maritimum* complex. Evanescent leaf bases have also been noted in *T. debile*, although Howell (1947) remarks that this feature is present only in *T. concinnum*. Persistent, fibrous leaf bases are apparent on all members of the *T. maritimum* complex but may be scarce on some specimens of *T. gaspense*. The paucity of fibrous bases, however, is probably related to the collecting practices of botanists or the amount of abrasion by sand, silt and water experienced by a particular plant, rather than being a character with any genetic basis.

7. LEAF SHAPE. Terete as opposed to compressed leaf blades have also been used as a diagnostic character in *Triglochin debile* and *T. gaspense*. The shape of leaves is a difficult character to evaluate on dried pressed specimens. Sections cut from field collections indicated that both these leaf shapes may be found in any one of the taxa; furthermore, they suggested that terete and compressed leaf blades represented extremes in a morphological continuum rather than discrete character states.

8. POLLEN DIAMETER. Slides of pollen were prepared with methyl green in glycerine jelly according to the method outlined by Radford et al. (1974). Twenty-five pollen grains per OTU were measured and the range and mean were calculated for each plant. The mean pollen size from each plant was then used to determine the range of means, grand mean, standard deviation and standard error for each taxon.

In their description of taxonomic characters, Löve and Lieth (1961) stated:

> "By measuring the size of the pollen in all available, fresh as well as preserved, material of *Triglochin*, we have found a good correlation between chromosome number and pollen size. If other morphological characters fail to give a conclusive indication of whether, for example, a plant is *T. debile* or *T. elatum* or *T. maritimum*, the pollen diameter can be used as evidence."

Pollen sizes are compared in Table 2. A one-way analysis of variance (ANOVA) and Scheffe's procedure (Maxwell, 1983) indicated the presence of three groups of pollen sizes. *Triglochin elatum* (coastal) had significantly larger pollen ($P < 0.05$) than any of the other taxa with a grand mean of 32.6 ± 3.3 μm. *Triglochin gaspense* possessed the second largest pollen with a grand mean of 29.8 ± 1.8 μm. *Triglochin debile*, *T. maritimum* and *T. elatum* (inland) had statistically similar pollen size ($P < 0.05$) with grand means of 27.0 ± 2.2, 27.2 ± 2.2 and 27.2 ± 1.8 μm, respectively. The ranges of diameters and range of means were found to overlap amongst all taxa.

The results of the pollen study can be contrasted with those of Löve and Lieth (1961) in Table 3. The ranges presented for the various taxa compare closely with those obtained in this study, as do the average pollen sizes for *Triglochin gaspense*, *T. debile* and *T. elatum*. However, the large pollen "characteristic" of *T. elatum* was evident only in *T. elatum* (coastal). The average pollen diameters found in *T. maritimum* and *T. elatum* (inland) are not comparable

Table 2. Comparison of pollen diameters for members of the *Triglochin maritimum* complex.

Taxa	Grand $\bar{x}$ (μm)	SD μm)	SE	Range of $\bar{x}$ (μm)	Range of diam. (μm)
T. debile	27.0	2.2	0.4	22.5-31.0	19.2 37.2
T. elatum (coastal)	32.6	3.3	0.7	26.1-39.8	21.6 44.4
T. elatum (inland)	27.2	1.8	0.4	24.9-31.3	21.6-36.0
T. gaspense	29.8	1.8	0.4	26.3 33.0	24.0 37.2
T. maritimum	27.2	2.2	0.4	21.7-32.3	18.0 36.2

Table 3. Comparison of pollen diameters for members of the *Triglochin maritimum* complex as determined by Löve and Lieth (1961).

Taxa	$\bar{x}$ (μm)	SD	Range of diam. (μm)
T. debile	26.8	0.1	21.8-32.3
T. elatum	33.4	0.2	26.3-39.8
T. gaspense	29.2	0.1	24.8-35.3
T. maritimum	24.8	0.2	20.3 32.3

between the two studies. It is important to note that the standard deviations given by Löve and Lieth are one order of magnitude smaller than the values obtained in this study and do not equate with the ranges they have depicted in their paper. The anomalies within their study as well as the discrepancies between our papers are difficult to reconcile without a detailed account of their sampling procedure.

In summary, it is evident that on the basis of pollen grain diameters, *Triglochin elatum*, *sensu* Löve and Lieth, is restricted to coastal areas of eastern North America and is not found inland . It is also apparent that *T. elatum* (inland), *T. debile* and *T. maritimum* do not exhibit distinct pollen sizes, as is stated by Löve and Lieth (1961), and are not significantly different ($P < 0.05$) from each other. This finding would seem to indicate that either pollen diameter does not reflect ploidy, or that the various cytotypes described by the Löve and Löve (1958) are not common and that the *T. maritimum* aggregate in eastern and central North America and Europe is represented primarily by three cytotypes. It is also evident from this study that pollen diameter is highly variable and of limited taxonomic use even in distinguishing *T. elatum* (coastal) and *T. gaspense* with certainty.

9. STIGMA CHARACTERS. Löve and Lieth (1961) stated that the stigmas in *Triglochin elatum* tend to be horizontal, while those in *T. gaspense* are usually bent at a 45° angle. In all 5 taxa this character was found to be highly variable with a range of angles, from 0 to 45, often found on the 6 carpels of one individual.

Differences in stigma neck length are also stated to occur between the taxa. It is difficult, however, to distinguish where the stigma neck ends and the main body of the carpel begins, making the measurement of this character highly subjective.

The maximum length of the papillae on the stigmatic surface provided a good distinction between some of the taxa. *Triglochin elatum* (coastal) and *T. elatum* (inland) have relatively long papillae, averaging 0.55 + 0.15 and 0.57 ± 0.19 mm, respectively. The papillae of *T. debile* and *T. maritimum* averaged about half this length with values of 0.35 ± 0.18 and 0.25 ± 0.12 mm being found respectively. *Triglochin gaspense* could usually be distinguished by its very

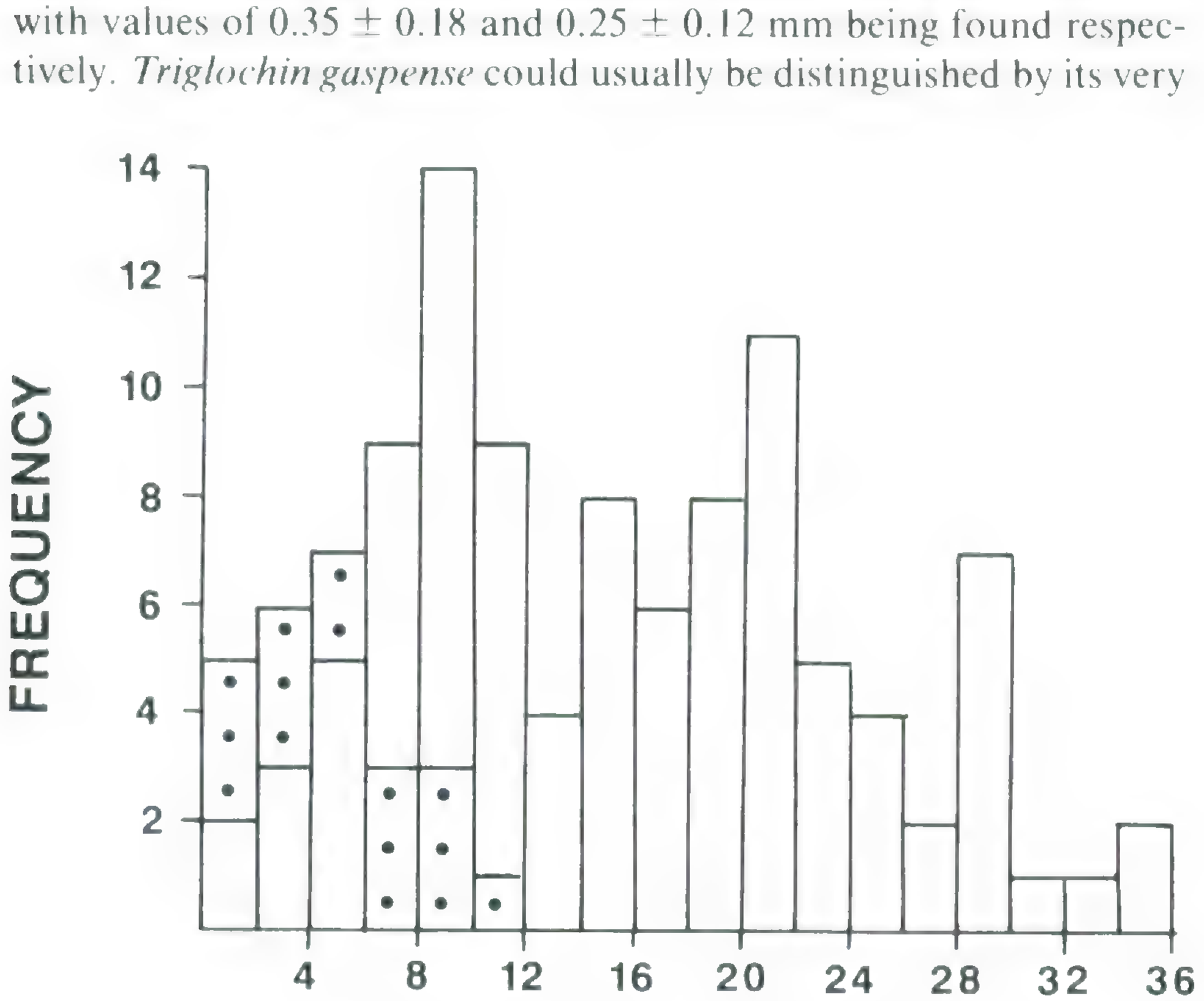


Figure 4. Frequency diagram of stigma papillae lengths in *Triglochin gaspense* ⊡ and the non-*gaspense* taxa □, for all flowering specimens examined (n = 125).

short papillae that averaged 0.16 ± 0.07 mm; however, short papillae could be found on the other taxa (Figure 4). In all cases the longest papillae on a plant were measured. Stigmatic papillae are an extremely ephemeral character and are not present on senescent flowers or mature fruits.

10. RACEME DENSITY. Raceme density was measured by counting the number of pedicels occurring in a 25 mm length. This count was taken from the middle of the raceme to avoid variations found at the extremes. *Triglochin gaspense* was distinguished by having more open racemes than other members of the complex, with an average of 8.6 ± 2.5 pedicels in flowering and 10.7 ± 3.4 pedicels in fruiting plants. The other taxa were characterized by having much denser racemes, this density being particularly pronounced in some specimens of *T. debile*, However, there is an overlap in pedicel density between all taxa (Figure 5).

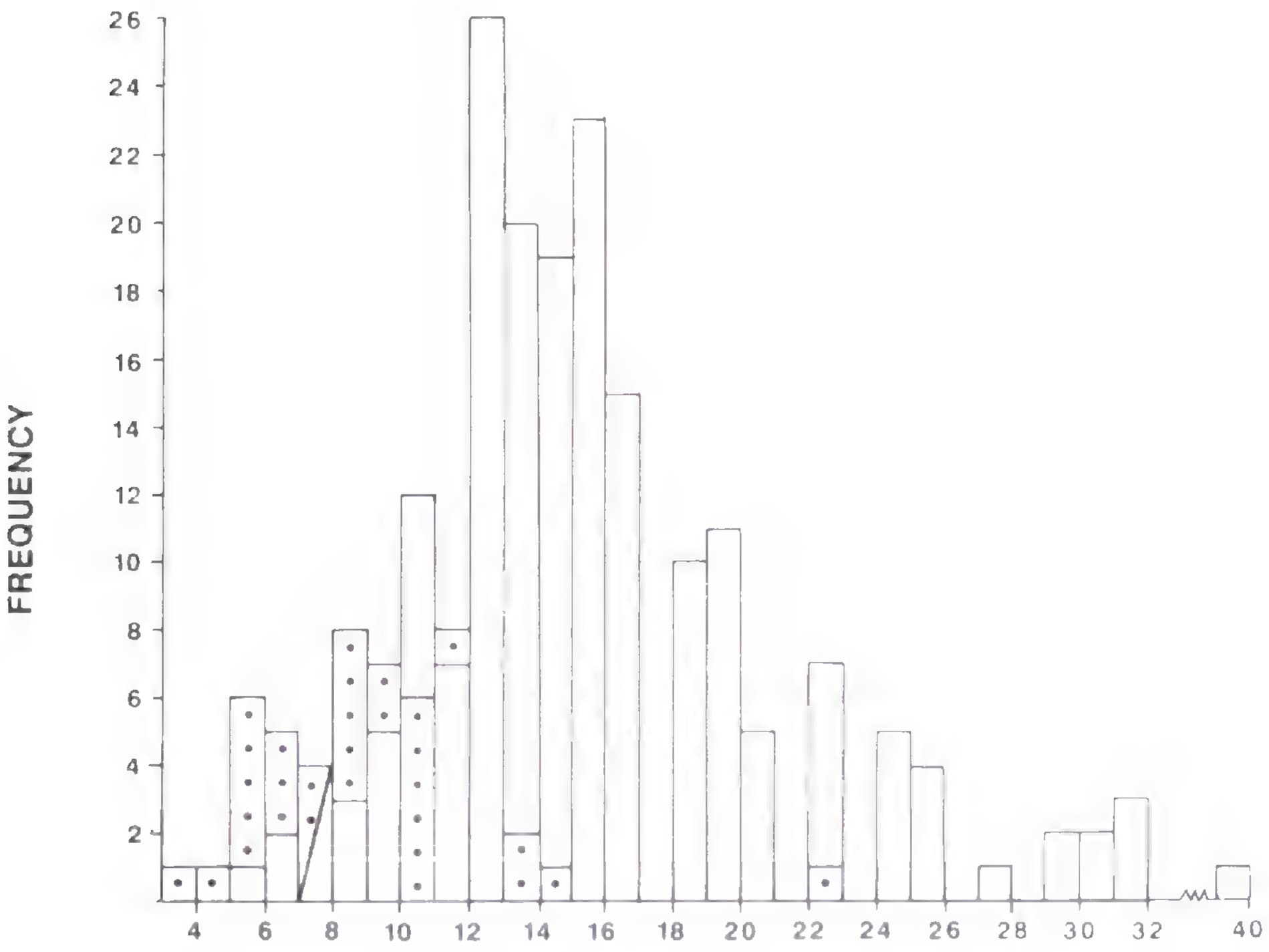


Figure 5. Frequency diagram of the number of pedicels in 25 mm interval along the scape in *Triglochin gaspense* ⊡ and the non-*gaspense* taxa □, for all flowering and fruiting specimens examined (n = 250).

11. CARPELS. Members of the *Triglochin maritimum* complex possess 6 carpels, although 3–12 have been observed in *T. gaspense* (Löve and Lieth, 1961; Fernald, 1903). The reason for carpel number variation in *T. gaspense* is not fully known but it is not thought to be correlated with the "unfavourable habitat" in which it grows (Fernald, 1903). Most of the plants observed in this study had 6 carpels. Although carpel length has been used in some keys there are only minor differences between the taxa.

Numerical Analyses

The first stage of the multivariate analysis provided a preliminary indication of the variability of the taxa in the *Triglochin maritimum* complex and the differences and similarities between them. The results of the PCA and DFA on 50 flowering OTUs disclosed that *T. gaspense* was relatively distinct from the rest of the *T. maritimum* complex. There was some degree of separation of the other taxa but it was not complete. It was also clear that taxa segregated on the basis of pollen diameter, in addition to geography, failed to separate clearly or to exhibit other character discontinuities. Therefore pollen was not used as a group-forming character in subsequent analyses.

During the second stage of the analysis, the PCA of the 138 flowering OTUs indicated the presence of two groups, segregating on the first principal component (PC) (Figure 6). While *Triglochin elatum* (inland), *T. elatum* (coastal), *T. debile* and *T. maritimum* did not separate, there was almost complete separation of *T. gaspense* toward the negative end of PC I although a few OTUs (42, 86, 99, 116, 118, 122) prevented complete separation of this group. The 13 OTUs from St. Omer, collected along a tidal gradient, clustered into two groups. Ten were placed with *T. gaspense* and three (136, 137, 138) with other members of the complex. The loadings given to each character indicated that all variables except pollen diameter contributed to the variation accounted for by the first axis. PC I accommodated 47.11% of the variation in the data set.

PC II and III respectively accounted for 19.01 and 10.25% of the variation in the data set, with PC III describing the most taxonomically useful variation. This axis provided partial separation of the non-*gaspense* taxa with *Triglochin elatum* (coastal) occurring toward the negative end and *T. debile* and *T. maritimum* toward the positive end of the third axis. The complete separation of two or more taxon clusters was not achieved, however (Figure 6). The

variables with the highest loadings on PC III included tepal, stamen, and papillae lengths and pollen diameter. The overlap that existed between the non-*gaspense* taxa did not disappear when PC IV was examined or in another analysis in which *T. gaspense* and St. Omer plants were excluded from the data set.

Two groups were evident in the DFA of the flowering data (Figure 7). The OTUs classified as *T. gaspense* occurred toward the negative end of canonical variate (CV) I, while other members of the *Triglochin maritimum* complex were segregated toward the positive end of this axis. *Triglochin elatum* (coastal) and *T. debile* were found at opposite ends of CV II, while *T. maritimum* and *T. elatum* (inland) were grouped toward the center of this axis. The dispersion of non-*gaspense* OTUs along with the high percentage of misclassifications (>25%) indicated the merger of these taxa. On the other hand, 92% of the *T. gaspense* OTUs were correctly classified (OTUs 118 and 122 were grouped with *T. maritimum*). Significant differences were found among the means of all taxa ($P < 0.001$; df = 5,116), although the difference between *T. debile* and *T. maritimum* was significant only at the 0.01 level ($F = 3.89$).

As was indicated by the PCA, some *Triglochin elatum* (coastal) and *T. maritimum* OTUs failed to segregate clearly from *T. gaspense*. This same pattern was again evident in the DFA, where OTUs 32, 42 and 86 were grouped with *T. gaspense*. Apparent misclassifications of certain OTUs in the discriminant space were probably related to the elimination of the leaf/scape variable in this analysis. The OTUs from the St. Omer plants were not used in the DFA but were assigned to groups on the basis of the classification of the five taxa. The same 10/3 split as was seen in the PCA was evident with OTUs 136, 137, and 138 being classified with non-*gaspense* taxa. Five variables were included in the discriminant function, and in order of importance were: spike density, leaf angle, stamen length, pollen diameter, and papillae length.

The analysis of the fruiting data set using PCA showed patterns similar to those found with flowering material, although the distinction between *Triglochin gaspense* and other members of the *T. maritimum* complex was not as clear. In this PCA, *T. gaspense* was found toward the negative end of PC I with all other taxa segregated toward the positive end. Several OTUs of *T. maritimum* and *T. elatum* (coastal), however, (particularly 182, 187, 220, 223) prevented the clear separation of taxon clusters. Five out of 11 OTUs from the St. Omer plants were classified with non-*gaspense* taxa

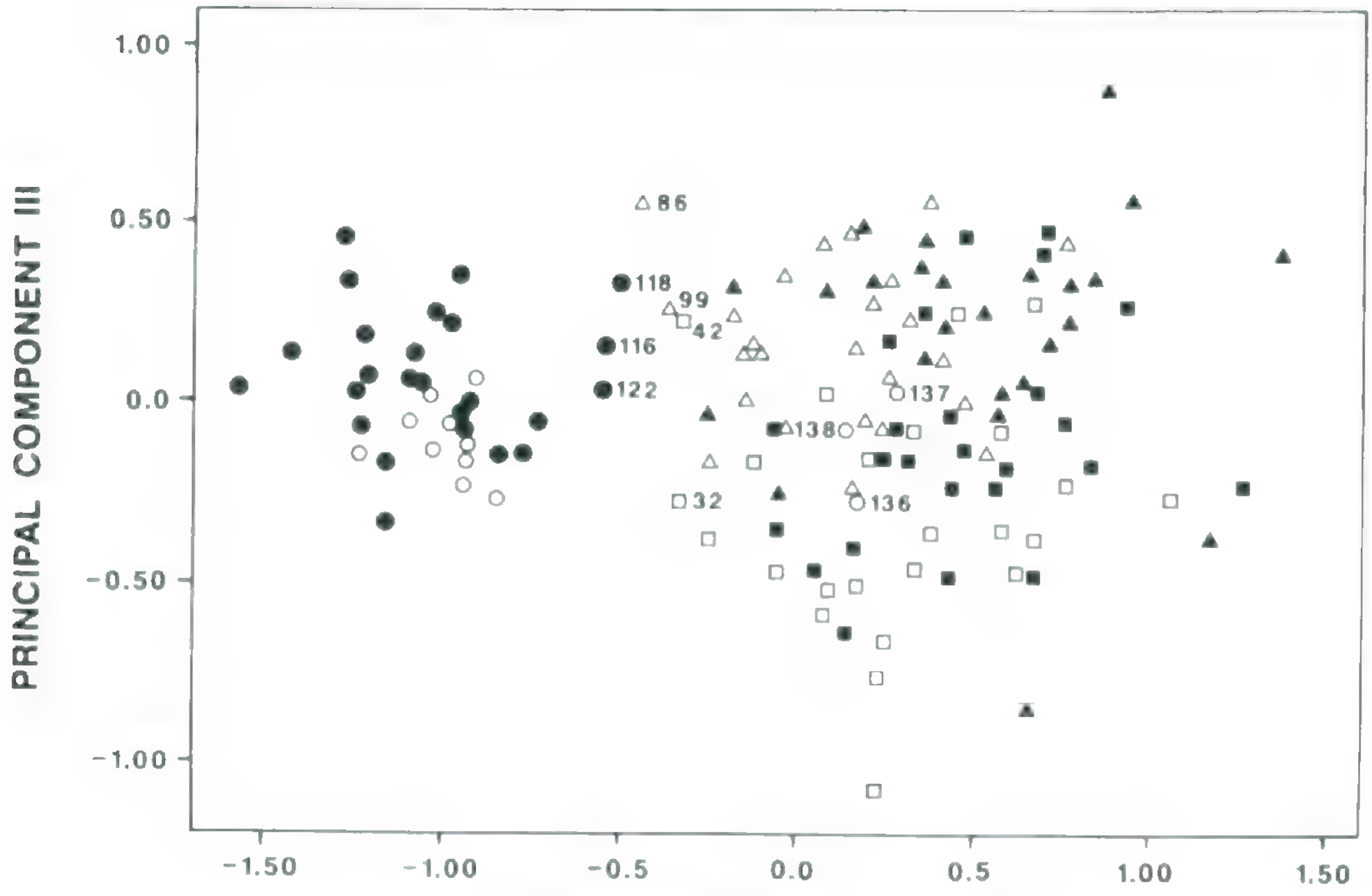


Figure 6. Bivariate plot of flowering OTUs on the first and third principal components. *Triglochin debile* ▲, *T. elatum* (coastal) □, *T. elatum* (inland) ■, *T. gaspense* ●, *T. maritimum* Δ, St. Omer plants ○.

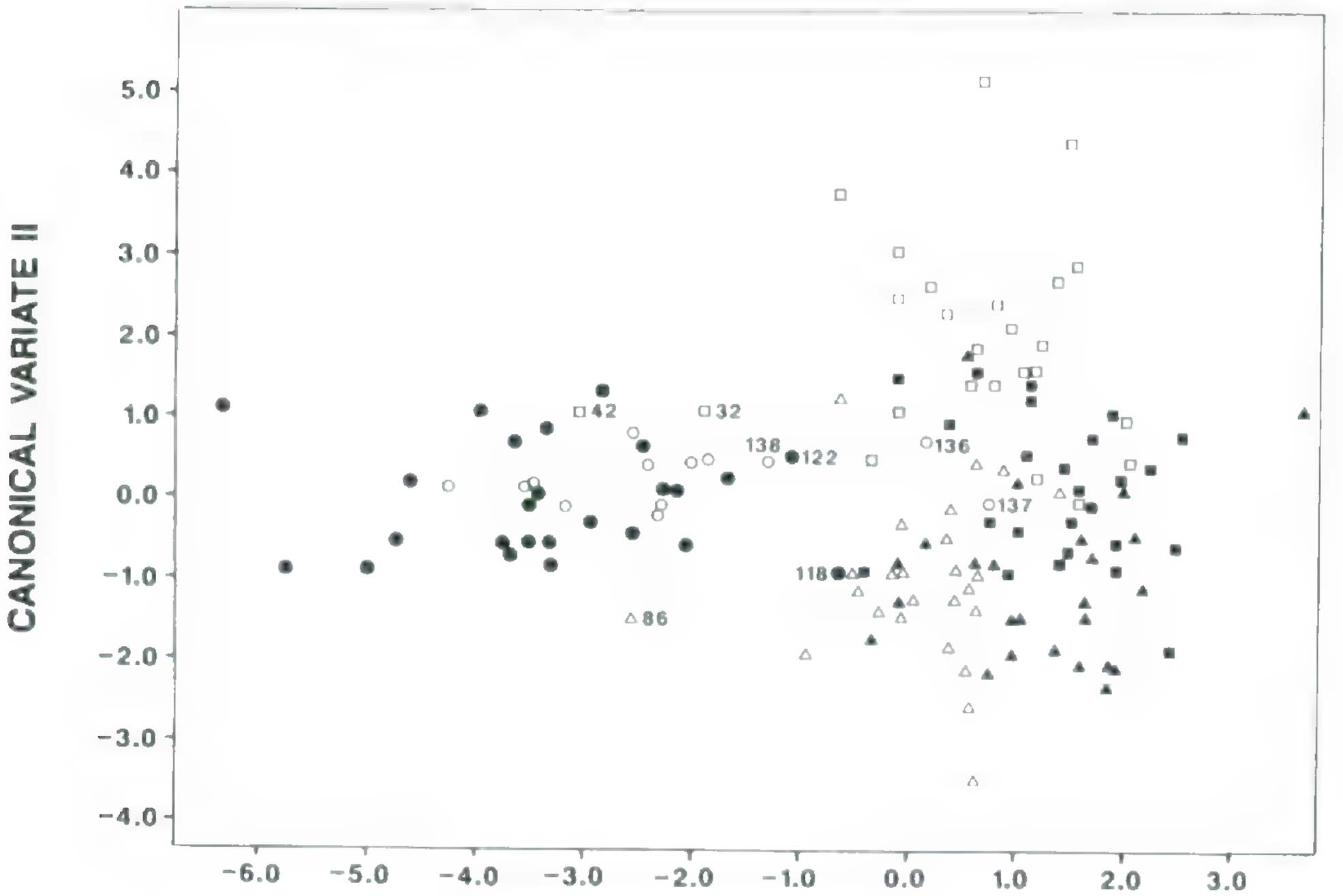


Figure 7. Bivariate plot of flowering OTUs on canonical variate I and II. *Triglochin debile* ▲, *T. elatum* (coastal) □, *T. elatum* (inland) ■, *T. gaspense* ●, *T. maritimum* Δ, St. Omer plants ○.

(269, 271, 272, 273, 274) (Figure 8). All characters contributed to the variation found on the first axis, with positive signs associated with most variables except leaf angle and leaf, scape scores. The first axis accounted for 51.05% of the variation in the data set.

PC II accommodated 22.19% of the variation in the data set with high positive values given to carpel length and seed length. A high negative loading was associated with spike density. PC II gave partial separation of the non-*gaspense* taxa, but, as in the flowering data analyses, separation of taxon clusters was not achieved (Figure 8). Dispersion of the non-*gaspense* taxa was not enhanced on axes III or IV or in an analysis in which *Triglochin gaspense* and St. Omer plants were removed from the data set.

The partitioning of OTUs in the DFA of the fruiting data set was based upon leaf angle, scape width, seed length and scape length.

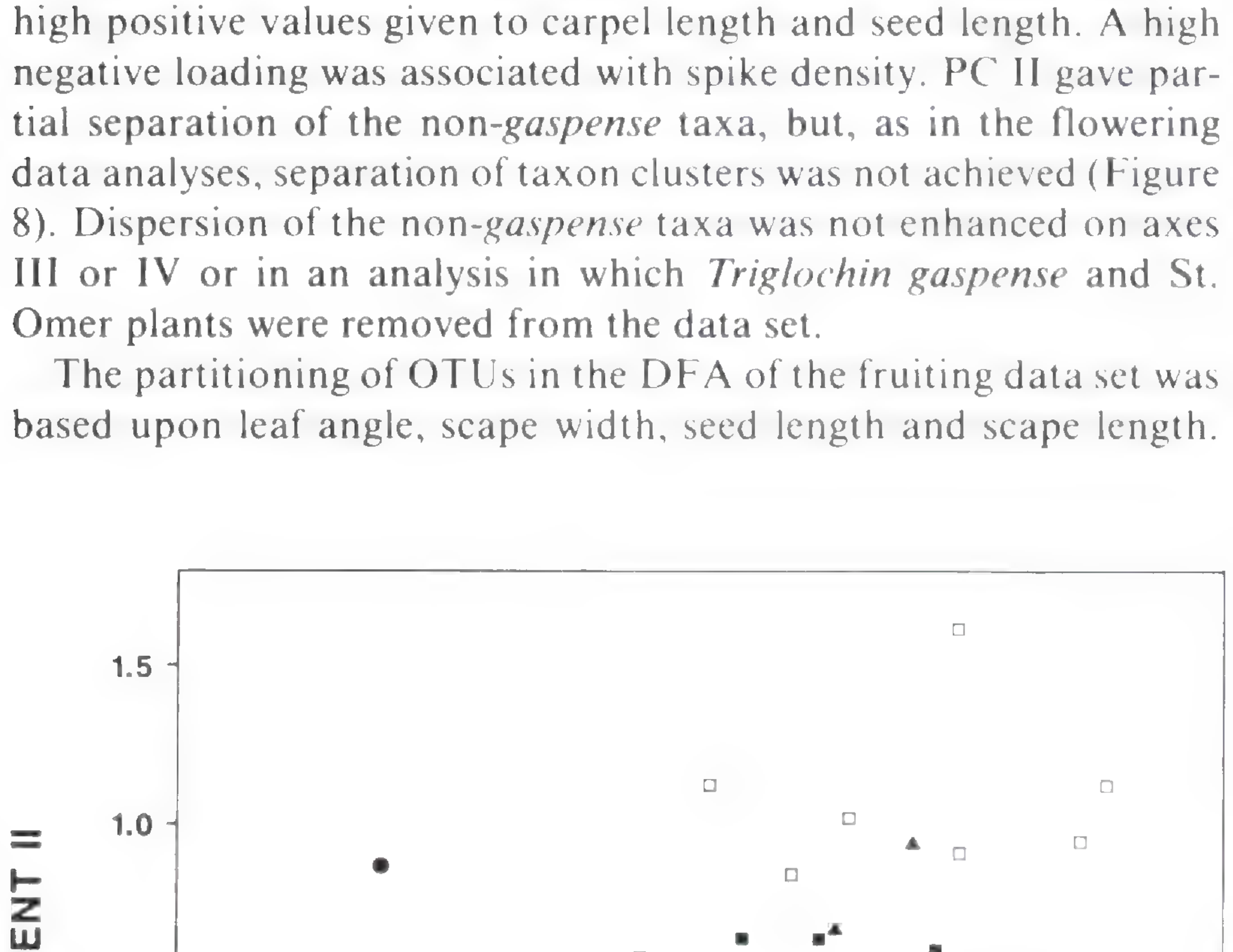


Figure 8. Bivariate plot of fruiting OTUs on the first and second principal components. *Triglochin debile* ▲, *T. elatum* (coastal) □, *T. elatum* (inland) ■, *T. gaspense* ●, *T. maritimum* Δ, St. Omer plants ○.

CV I produced a continuum of OTUs with *Triglochin gaspense* tending to fall toward the negative pole, and the non-*gaspense* taxa grouping toward the positive end (Figure 9). CV II failed to provide efficient separation of taxon clusters. Only 84% of the *T. gaspense* OTUs were correctly classified, with misclassified specimens placed with *T. elatum* (coastal) (239, 243, 245) and *T. maritimum* (263). OTU 187 was grouped with *T. maritimum*, while two *T. maritimum* OTUs, 221 and 223, were classified as *T. gaspense*. Four St. Omer OTUs were classified as belonging to taxa other than *T. gaspense* (265, 269, 270, 271). OTUs 272, 273 and 274, which had been grouped with non-*gaspense* taxa in the PCA, were classified with *T. gaspense* in the DFA.

The results of stage two of the multivariate analyses indicated the presence of two groups in the *Triglochin maritimum* complex; however, the distinction between *T. gaspense* and *T. maritimum*/*T. elatum* (coastal) was not absolute. In order to explore this relationship further a series of pairwise comparisons including *T. gaspense* and St. Omer plants as one group and either *T. elatum* (coastal) or *T. maritimum* as the other were conducted using

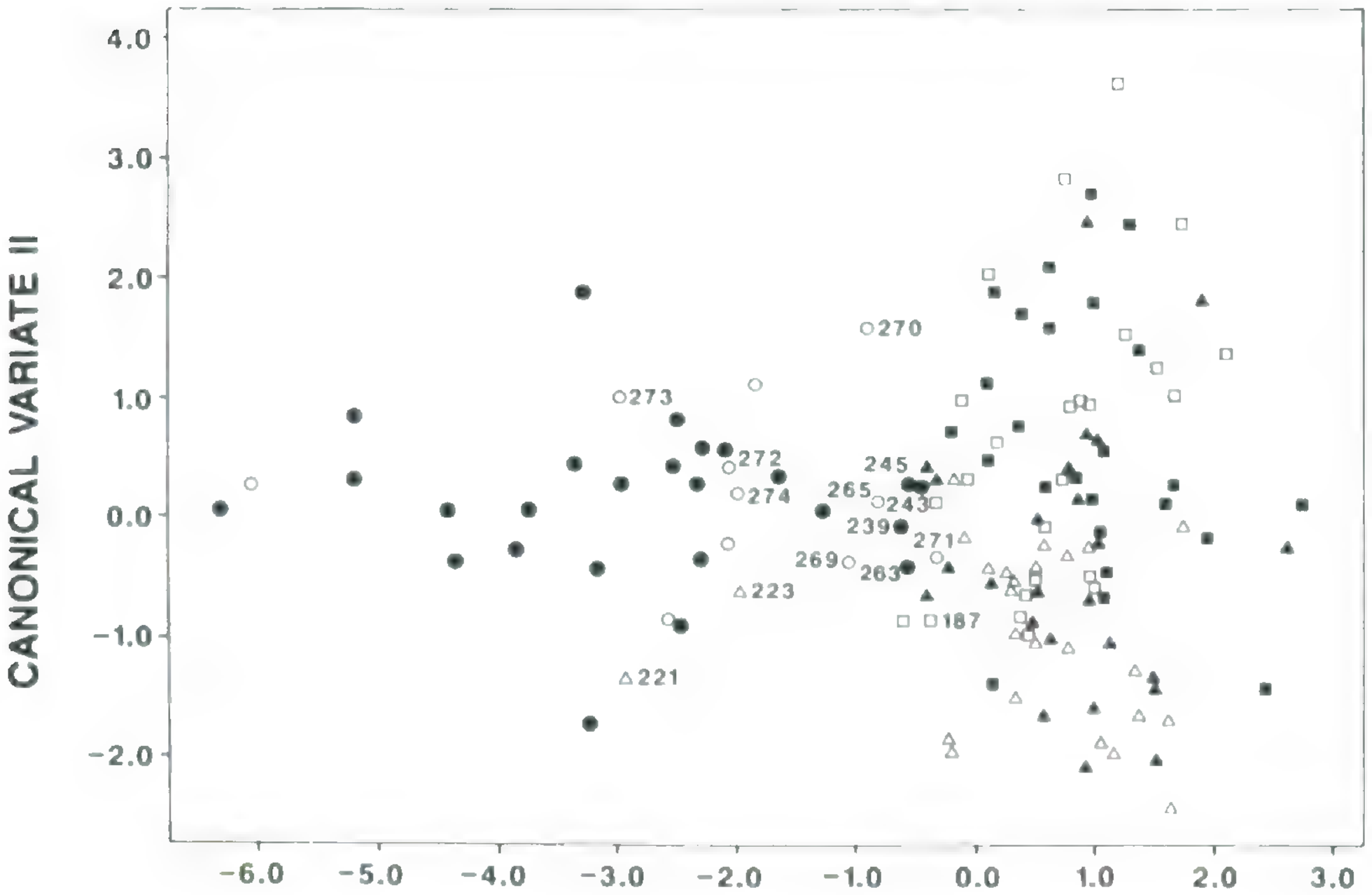


Figure 9. Bivariate plot of fruiting OTUs on canonical variate I and II. *Triglochin debile*▲, *T. elatum* (coastal) □ , *T. elatum* (inland) ■, *T. gaspense* ● *T. maritimum*Δ, St. Omer plants ◯ .

UPGMA, PCA and DFA. Although these analyses indicated two distinct clusters of OTUs, separation of the taxa was not improved over that depicted in the original PCAs (Figures 6 and 8).

TAXONOMIC TREATMENT

The results of this study indicate the presence of two taxa in eastern and central North America and Europe: *Triglochin gaspense* and *T. maritimum* (incl. *T. elatum* and *T. debile*). *Triglochin gaspense* is usually segregated from the other taxa in the numerical analyses, suggesting that it should continue to be recognized at the specific level. This conclusion is also supported to some extent by its ecological and geographic differentiation (*see* below).

The numerical analyses failed to differentiate satisfactorily between *Triglochin elatum* (coastal), *T. elatum* (inland), *T. debile* and *T. maritimum*, although different chromosome numbers are known to exist within this group. Although *T. elatum* (coastal) has large pollen and *T. debile* is inclined to have densely flowered racemes, they cannot be consistently recognized using these morphological trends and they should be treated as one species. Indeed, the separation is so unreliable that we are of the opinion that no useful purpose is served by recognizing these taxa at infraspecific rank either.

KEY TO THE SPECIES OF THE *TRIGLOCHIN MARITIMUM* GROUP IN EASTERN AND CENTRAL NORTH AMERICA AND EUROPE

A. Leaves equalling or longer than the scape, the blade patent and arcuate; scape 0.3–1.10 mm wide; stigmatic papillae short, 0.05–0.3 mm; raceme lax with 4–17 (24) flowers per 25 mm interval; plants restricted to the tidal zone of salt marshes in northeastern North America . . . . . 1. *T. gaspense*

A. Leaves usually shorter than the scape, the blade erect and straight; scape (0.7) 0.9–3.7 (4.2) mm wide; stigmatic papillae 0.08–0.9 mm; raceme dense with 6–30 (40) flowers per 25 mm interval; plants widespread . . . . . 2. *T. maritimum*

1. **Triglochin gaspense** Lieth and D. Löve, Canad. J. Bot. 39:1261. 1961. HOLOTYPE: Between Barchois-Ouest and Coin-du-Banc, Gaspé Peninsula. "Salt marsh below high-water mark." No. 60-0636, Lieth, Dansereau, Waltz, Ouelette. July 25, 1960 (MT!).

"*Triglochin concinna*" *sensu* Fernald, Gray's Manual of Botany: 83. 1950.

Caespitose, scapose perennial. Scape up to 220 mm high, terete, 0.3–1.1 mm wide. Leaves erect to patent and arcuate, terete to compressed in cross section, equalling or exceeding the scape. Ligule 0.3–1.5 mm long, obtuse, flat or cucullate at the apex. Raceme lax with 4–17 (23) flowers per 25 mm of the scape. Flowers perfect, on short pedicels. Tepals 6, in two series of three, deltoid, 1.4–2.2 mm long, translucent to opaque, tinged purplish or bronze, tips ± acute. Anthers ovate to broadly ovate, 0.8–1.4 mm long. Mean pollen diameter 26.3–33.0 μm. Carpels 6 (rarely 1–12), 3.1–4.5 mm long. Styles short, abruptly spreading into a more or less horizontal stigma. Stigma papillae 0.05–0.3 mm long, withering soon after anthesis. Seed cylindric, (1.4) 1.7–3.2 (3.4) mm long.

The holotype and paratypes as well as other material annotated by the authors are referable to *Triglochin gaspense*; however, one of the paratypes, *Donly 30,* July 17, 1956 (DAO), is *T. palustre*.

The present study has shown that while *Triglochin gaspense* is relatively distinct in the numerical analyses, no one character consistently distinguished this species. However, the combination of leaves longer than the scape, narrow scape width, patent, arcuate leaves, lax racemes and short stigmatic papillae, make *T. gaspense* a relatively distinct member of the *T. maritimum* complex. Misclassification of OTUs in the numerical analyses was primarily restricted to fruiting material and to the DFA of both data sets, in which certain key characters were excluded. However, some intermediates are apparent (e.g. OTUs 32, 42, 86, 99, 116, 118, 122) in the PCA of the flowering material. While detailed investigations of mixed populations of *T. gaspense* and *T. maritimum* may lead to modification of our classification, it appears that the vast majority of plants examined in this study can be identified with certainty.

Triglochin gaspense differs markedly from *T. maritimum* in its habitat. It is restricted to areas within the tidal zone below the high water mark of northeastern North America (Figure 10). It is often the dominant species in this habitat and is ecologically separated from *T. maritimum*. Common associates include *Plantago maritima* L., *Glaux maritima* L., *Spartina patens* (Ait.) Muhl. and *Salicornia* L. spp. (Thannheiser, 1981).

Rouleau's (1978) treatment of *Triglochin gaspense* as a hybrid between *T. palustre* and *T. maritimum* is interesting, but conclusions based on this study indicate that he is probably incorrect. Although *T. gaspense* is small in stature and has lax racemes like *T.*

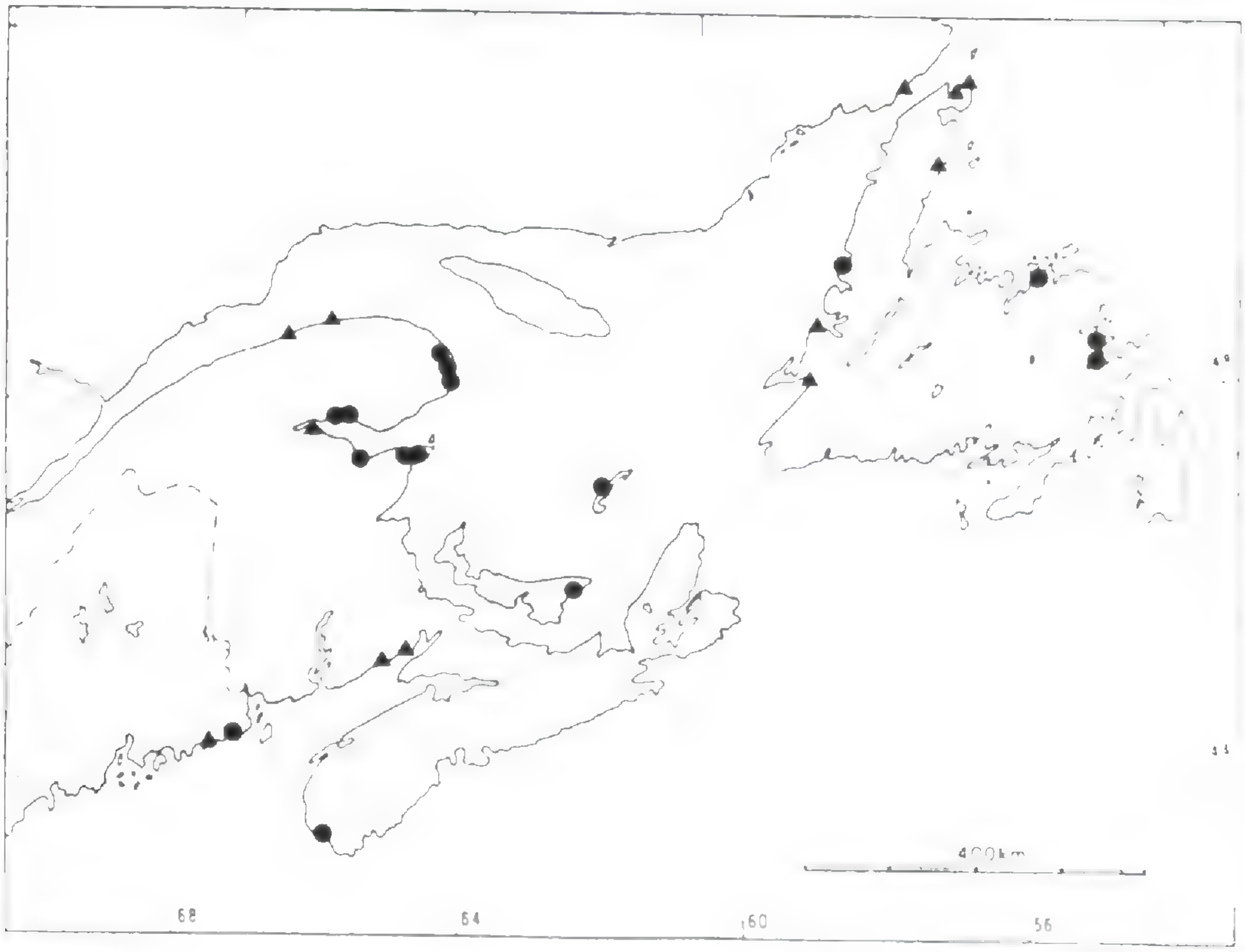


Figure 10. Distribution of *Triglochin gaspense*. Specimens examined ●, records published by Thannheiser (1981), Crow and Hellquist (1982) and Hinds (1986)▲.

palustre, characters such as patent leaves that are longer than the scape appear to be unique to this species. Furthermore, fruit and flower morphology are not intermediate between the putative parents. A search for *T. palustre* at many of the *T. gaspense* stations indicated that it was rare or absent and when present was not found in the ecotone separating *T. gaspense* and *T. maritimum*.

2. **Triglochin maritimum** Linnaeus. Sp. Pl. 339. 1753. HOLOTYPE: 2. *maritimum*, Savage Cat. Linn. Herb. # 466.20. LINN, photo TRT!

Triglochin elatum Nuttall. Gen. N. Amer. Pl. 237. 1: 1818 HOLOTYPE: "New York State, lit. and marshes." (PH!).

Caespitose, scapose perennial. Scape up to 1200 mm high, terete, (0.7) 0.9–3.7 (4.2) mm wide. Leaves erect, straight, terete to compressed in cross section, much shorter than or equalling the scape. Ligule 0.7–2.6 mm long, obtuse to acute, sometimes bilobed. Raceme usually dense, with 6 30 (42) flowers per 25 mm interval of the scape. Flowers perfect, on short pedicels. Tepals 6 in two series

of three, deltoid, 1 2 2.7 mm long, translucent to opaque, tinged purplish or bronze, tips ± acute. Anthers ovate to broadly ovate, 0.6 1.8 (2.0) mm long. Mean pollen diameter, 21.7 35.3 (39.8) μm. Carpels 6, 2.9 5.8 (7.0) mm long. Styles short, abruptly spreading into a more or less horizontal stigma. Stigmatic papillae 0.08 0.9 mm, withering soon after anthesis. Seed cylindric, 1.7 3.8 (4.6) mm long.

There appears to be some discrepancy over the spelling of the specific epithet in much of the literature reviewed in this study. As Voss (1966) has pointed out, both epithets were given neuter form by Linnaeus (*Glochis*, in contrast to *triglochin*, is chiefly feminine). Since Linnaeus employed the neuter gender *Triglochin*, the specific epithet is correctly *maritimum* not *maritima*; this consistency also applies to the specific epithets *concinnum* and *elatum*.

The numerical analyses failed to fully differentiate any of the non-*gaspense* taxa, despite the rather high morphological variability found in this group. The polyploid nature of this species, its wide distribution and adaptation to both fresh and salt water environments could be contributing factors to this diversity, since morphological variability does seem to follow a weakly defined trend. *Triglochin maritimum* (*sensu stricto*) tends to be a smaller plant than other segregates, while *T. debile* is inclined to have more densely flowered racemes. Plants of *T. elatum* (both inland and coastal) have longer stigmatic papillae than other members of the complex with coastal plants having much larger pollen. However, the lack of clear differentiation between these plants indicates that they are best treated as a single polymorphic species, rather than as separate taxa.

While plants from central North America, referred to as *Triglochin debile* by Löve and Löve (1958), are best recognized as *T. maritimum*, this name was not placed in synonymy because the type locality of *T. debile* is from Utah, a geographic region not extensively surveyed in this study. Since Howell (1947) has transferred this plant to a variety of *T. concinnum*, it is possible that the name *T. debile* has been applied in a much broader sense than was originally intended and refers only to those plants from the North American southwest. The relationship of *T. debile* to *T. maritimum* necessitates a detailed comparision with *T. concinnum* before its true taxonomic affinities can be ascertained.

Triglochin maritimum is found in a variety of neutral to alkaline, fresh and saltwater habitats that include brackish marshes, sloughs, ditches, fens and shorelines. Where *T. maritimum* is sympatric with

T. gaspense they are ecologically separated, with *T. maritimum* growing in drier, less disturbed portions of the marsh, above the high water mark. In eastern North America, *T. maritimum* ranges as far north as the tree line and south to the lower Great Lakes. It is absent from the Appalachian mountain region, but extends southward along the Atlantic coast to New Jersey. In central North America, *T. maritimum* has a much more southerly distribution and is found as far south as New Mexico. Distribution maps of *T. maritimum sensu lato* are provided by Hultén (1962, 1968) and Porsild and Cody (1980).

ACKNOWLEDGMENTS

We acknowledge the help of the curators of CAN, DAO, MT and TRT for expediting loans. We especially thank Stuart Hay (MT) for tracking down the type of *Triglochin gaspense* and for drawing relevant literature to our attention. The helpful comments and invaluable field assistance of John A. Ford were also greatly appreciated. This work was supported by National Research Council of Canada Grant A6494 to P. W. B.

LITERATURE CITED

Catling, P. M., D. S. Erskine, and R. B. Maclaren. 1985. The plants of Prince Edward Island with new records, nomenclatural changes, and corrections and deletions. Publication 1798. Research Branch, Agriculture Canada, Ottawa.

Crow, G. E., and C. B. Hellquist. 1982. Aquatic Vascular Plants of New England: Part 4. Juncaginaceae, Scheuchzeriaceae, Butomaceae, Hydrocharitaceae. Station Bulletin 520. New Hampshire Agricultural Experiment Station, University of New Hampshire, Durham.

Dandy, J. E. 1980. *Triglochin*. In: "Flora Europea. Vol. 5. Alismataceae to Orchidaceae (Monocotyledons)," (Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, D. A. Webb, Eds. Cambridge University Press, Cambridge, England.

Davy, J. B. 1895. Plants hitherto undescribed. Erythea, 3: 116 118.

Dixon, W. J., Ed. 1983. BMDP Statistical Software. 1983 revised printing. University of California Press, Berkeley.

Erskine, D. S. 1960. The plants of Prince Edward Island. Publication 1088. Plant Research Institute, Research Branch, Canada Dept. of Agriculture, Ottawa.

Fernald, M. L. 1903. Some variations in *Triglochin maritima*. Rhodora 5: 174-175.

———. 1950. Gray's Manual of Botany. 8th ed. Van Nostrand Reinhold Co. New York.

Gleason, H. A. 1952. Illustrated Flora of the Northeastern United States and Adjacent Canada. 3rd ed. Lancaster Press, Inc. Lancaster, PA.

GRAY, A. 1856. Manual of the Botany of the Northern United States. Rev. ed. New York.

_____. 1889. Manual of the Botany of the Northern United States. 6th ed. Rev. by S. Watson and J. M. Coulter. New York.

HINDS, H. R. 1983. The rare vascular plants of New Brunswick. Syllogeus. 50.

_____. 1986. The Flora of New Brunswick. Primrose Press, Fredericton, New Brunswick.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, AND J. W. THOMPSON. 1971. Vascular Plants of the Pacific Northwest. Part 1. University of Washington Press, Seatle.

HOLMGREN, P. K., W. KEUKEN, AND E. K. SCHOFIELD. 1981. Index Herbariorum. Part I. The Herbaria of the World. Regnum Vegetabile, Vol. 106.

HOWELL, J. T. 1947. Remarks on *Triglochin concinna*. Leaflets of Western Botany 5: 13–19.

HULTÉN, E. 1962. The circumpolar plants. I. Vascular cryptogams, conifers, monocotyledons. K. Sven. Vetenskapsakad. Handl. ser. 4, 8 (5): 1–275.

_____. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, CA.

JONES, M. E. 1895. Contributions to western botany. VII. Proc. Calif. Acad. Sci. Ser. 2, 5: 611–732.

KAUL, R. B. 1986. Juncaginaceae Rich., the arrowgrass family. *In:* Flora of Great Plains, R. L. McGregor, Coordinator. University Press of Kansas, Lawrence, Kansas.

LINNAEUS, C. 1753. Species Plantarum. Vol. 1. Holmiae.

LOOMAN, J. 1976. Biological flora of the Canadian Prairie Provinces. IV. *Triglochin* L., the genus. Canad. J. Plant Sci. 56: 725 732.

LÖVE, D. AND H. LIETH. 1961. *Triglochin gaspense,* a new species of arrow grass. Canad. J. Bot. 39: 1261–1272.

LÖVE, A., AND D. LÖVE. 1958. Biosystematics of *Triglochin maritimum* agg. Naturaliste Canad. 53: 877–893.

MASON, H. L. 1957. A Flora of the Marshes of California. University of California Press, Berkeley and Los Angeles.

MAXWELL, E. A. 1983. Introduction to Statistical Thinking. Prentice-Hall Inc. Englewood Cliffs, N.J.

MOSS, E. H. 1983. Flora of Alberta. 2nd. ed., rev. by J. G. Packer. University of Toronto Press, Toronto.

MUNZ, P. A. 1963. A California Flora. University of California Press, Berkeley and Los Angeles.

NUTTALL, T. 1818. The Genera of North American Plants, and a Catalogue of the Species to the Year 1817. Vol. I. Philadelphia, PA.

PORSILD, A. E. AND W. J. CODY. 1980. Vascular Plants of the Continental Northwest Territories, Canada. Canad. Natl. Mus. Nat. Sci.

RADFORD, A. E., W. C. DICKINSON, W. C. MASSEY, AND C. R. BELL. 1974. Vascular Plant Systematics. Harper and Row, New York.

ROHLF, F. J., J. KISHPAUGH AND D. KIRK. 1982. Numerical Taxonomy System of Multivariate Programs. State University of New York, Stony Brook.

ROLAND, A. E., AND E. C. SMITH. 1969. The Flora of Nova Scotia. The Nova Scotia Museum, Halifax.

ROULEAU, E. 1978. List of the Vascular Plants of the Province of Newfoundland (Canada). Oxen Pond Botanic Park, St John's, Nfld.

ROUSSEAU, C. 1974. Géographie floristique du Québec/Labrador. Distribution des principales espèces vascularies. Les Presses de l'Université Laval. Québec.

SCOGGAN, H. J. 1978. The Flora of Canada. Part 2. Pteridophyta, Gymnospermae, Monocotyledoneae. Canad. Natl. Mus. Nat. Sci. Publ. Bot. No. 7(2).

SEYMOUR, F. C. 1969. The Flora of New England. C. E. Tuttle Co. Rutland, VT.

THANNHEISER, D. 1981. Die Küstenvegetation Ostkanadas. Münstersche geographische Arbeiten Ferdinand Schöningh, Paderborn.

VAN BRUGGEN, T. 1976. The Vascular Plants of South Dakota. Iowa State University Press, Ames.

VOSS, E. G. 1966. Nomenclatural Notes on Monocots. Rhodora 68: 435 463.

———. 1972. Michigan Flora. Part I. Gymnosperms and Monocots. Cranbrook Inst. Sci. No. 55.

DEPARTMENT OF BOTANY
ERINDALE CAMPUS
UNIVERSITY OF TORONTO
MISSISSAUGA, ONTARIO
L5L 1C6

RHODORA, Vol. 90, No. 863, 1988

NEW ENGLAND NOTE

ASTER NEMORALIS IS EXTANT IN VERMONT

PETER F. ZIKA

Last recorded in Vermont in 1899, *Aster nemoralis* Aiton was known from a single collection at "North Pond, Brunswick" in Essex County (*Eggleston 1326* HNH, VT). This site was difficult to relocate, since North Pond was not shown on contemporary maps, such as U.S.G.S. topographics and the Vermont Atlas (Hancock et al., 1978).

In the course of exploring a number of ponds and wetlands in northeastern Vermont, five localities for *Aster nemoralis* were uncovered in Essex County, as follows:

Brighton, sandy and boggy shoreline of Nulhegan Pond, about 400 plants, *Zika 4246* (VT); Brunswick, boggy western margin of Dennis Pond, about 3000 plants, *Zika 4273* (NEBC, VT); Ferdinand, hummocks on shore of bog pond, Moose Bog, about 100 plants, *Zika 4160 & 4652A* (VT); Ferdinand, boggy shoreline of unnamed pond between Route 105 and Notch Pond Mountain, about 200 plants, *Zika 3628 & 4304* (VT); Maidstone, boggy west border of West Mountain Pond, about 500 plants, *Zika 6393* (VT).

Two of these sites could possibly be the historical locality, which was described as a rocky shoreline (Brainerd et al., 1900), but there is no way to tell with certainty.

From a regional perspective, *Aster nemoralis* is widespread and not rare, threatened or endangered. Pease (1964) reported six localities in adjacent Coos County, New Hampshire, and the species is known from every county in Maine (Richards et al., 1983). It also has a wide distribution in eastern Canada (Brouillet and Simon, 1981). Although *A. nemoralis* is a scarce species in Vermont, the known populations are remote and relatively safe from disturbance. I suggest that the species be considered rare, and not be considered a state threatened or endangered species requiring legislative protection.

LITERATURE CITED

BRAINERD, E., L. R. JONES AND W. W. EGGLESTON. 1900. Flora of Vermont. Free Press Association, Burlington.

BROUILLET, L. AND J. SIMON. 1981. An ecogeographical analysis of the distribution of *Aster acuminatus* Michaux and *A. nemoralis* Aiton (Asteraceae: Astereae). Rhodora 83: 521–550.

HANCOCK, W., P. LANE, L. HUNTINGTON AND J. E. KELLY. 1978. The Vermont Atlas and Gazetteer. David DeLorme Co., Yarmouth.

PEASE, A. S. 1964. A Flora of Northern New Hampshire. New England Botanical Club, Cambridge.

RICHARDS, C. D., F. HYLAND AND L. M. EASTMAN. 1983. Revised check-list of the vascular plants of Maine. Bull. Josselyn Bot. Soc. Maine 11: 1–73.

BUREAU OF LAND MANAGEMENT

P.O. BOX 10226

EUGENE, OR 97440

RHODORA, Vol. 90, No. 863, 1988

NEW ENGLAND NOTE

KUDZU (*PUERARIA LOBATA*) IN NEW ENGLAND

BRUCE A. SORRIE AND WILLIAM D. PERKINS

The eastern Asian climbing legume *Pueraria lobata* (Willd.) Ohwi, popularly known as kudzu, has been the object of much interest and concern in the United States. Originally introduced as an ornament and for its edible tuberous roots (Fernald et al., 1958), kudzu was later adopted for use in the southeastern United States as a stabilizer of disturbed soil, due to its rapid growth. However, the plant quickly spread from roadside banks and erosion gullies to fencerows and forests. Growth is so rapid and extensive as to completely cover and kill (by shading) tall trees. Now, costly eradication programs attempt to check its spread.

In the late summer of 1981 the authors independently discovered two different populations of kudzu in Plymouth County, Massachusetts. Collection details are as follows:

> Hull, Peddocks Island, vigorous in small area of former military residences, 5 September 1981 (flowers) *Perkins s.n.* (NEBC). Kingston, climbing abundantly over staghorn sumac, shrubs, and small trees, first road N of Plymouth town line, W of route 3A, 22 August 1981 (flowers) *Sorrie & Strawn 1224* (NEBC); 18 September 1981 (fruit) *Sorrie 1317* (NEBC); 22 October 1983 (fruit) *Sorrie 2307* (NEBC, MASS).

The Hull station is on an island that was used as a military fortification from about 1904 until shortly after World War II; kudzu was possibly introduced there by a soldier from the South. The Kingston station is adjacent to a Chinese restaurant and may have been planted there, since the powdered root is used in cooking (Shurtleff and Aoyagi, 1977).

To our knowledge these reports represent the northernmost stations in eastern North America. Inquiries to several herbaria in the region (including Canada) yielded no specimens from north of New Jersey. Our report of kudzu in New England is perhaps not surprising, for although leaves and young stems are highly frost-sensitive, older stems are able to withstand cold winters in southern and mid-Atlantic states (Duncan, 1967). In New England, apparently only the thick root is able to resist freezing. At both Plymouth County

stations kudzu grows luxuriantly during summer, flowers abundantly, and produces fruits. Seeds of the latter are apparently nonviable, for no seedling plants have been found. Plants grow 10–15 m before succumbing to autumn frosts. Plants die back to ground level each winter, even though the immediate proximity of the Atlantic Ocean tempers winter climatic conditions.

To these Plymouth County stations can be added seven other New England records:

Massachusetts: Plymouth County: Hingham, "cultivated," October 1943 (vegetative) *Davis s.n.* (MASS); Bristol County: Dartmouth, planted about 1940 in yard, dies back each winter, 7 November 1982 (vegetative) *Sorrie & Strawn 1874* (NEBC); Barnstable County: Orleans, climbing on *Celastrus orbiculatus* Thunb., 1987, Lawrence Mish (pers. comm.); Hampden County: Springfield, "cultivated," 19 August 1938 (vegetative) *Stark s.n.* (MASS). **Connecticut:** New Haven County: New Haven, overtopping three-story building behind health foods store, 1978–1985+, Lauren Brown (pers. comm.); Fairfield County: Fairfield, roadside, probably planted, Lauren Brown (pers. comm.).

The MASS specimens were originally determined as *Pueraria hirsuta* Schneid., a synonym of *P. lobata*. They are obviously specimens taken from cultivation, as stated on the labels.

From the above records, it appears that kudzu began to be cultivated as an ornamental in New England in the late 1930's. This conclusion is consistent with the time of the campaign by the U.S. Soil Conservation Service to promote kudzu as a soil binder (Shurtleff and Aoyagi, 1977). Seeds could then be obtained simply by request. More recent records apparently reflect the growing interest in health foods and oriental cuisine. Most of the New England records can be traced directly back to planted or discarded material and thus are best termed "persistent" following cultivation as opposed to "adventive" as ordinarily used in phytogeography. The apparent lack of viable seeds, coupled with above-ground dieback each winter, suggests that kudzu is unlikely to spread or to become a troublesome weed in New England.

ACKNOWLEDGMENTS

We wish to thank Patricia Swain and two anonymous reviewers for reviewing a draft of this note. We also with to thank the curators of the following herbaria for access to their holdings: CONN, GH, MASS, NEBC. Lauren Brown of Branford, Connecticut generously provided information that she has gathered regarding the Connecticut stations and Lawrence Mish shared his discovery of the Orleans, Massachusetts station.

LITERATURE CITED

DUNCAN, W. H. 1967. Woody vines of the southeastern states. Sida 3(1): 20–21.

FERNALD, M. L., A. C. KINSEY, AND R. C. ROLLINS. 1958. Edible Wild Plants of Eastern North America. Harper & Row, New York.

SHURTLEFF, W. AND A. AOYAGI. 1977. The Book of Kudzu: A Culinary and Healing Guide. Autumn Press, Brookline, Massachusetts.

B. A. S.
NATURAL HERITAGE AND ENDANGERED SPECIES PROGRAM
100 CAMBRIDGE ST.
BOSTON, MA 02202

W. D. P.
SOUTH STREET
HALIFAX, MA 02338

RHODORA, Vol. 90, No. 863, 1988

NEW ENGLAND NOTE

BETULA NIGRA AT MENDUM'S POND, BARRINGTON, NH AND PAWTUCKAWAY LAKE, NOTTINGHAM, NH

CHARLES R. CORMIER

On March 2, 1986 I went to Mendum's Pond to look for *Betula nigra* at the northeastern limit recorded by A. R. Hodgdon in 1958. I walked along the southeastern shore line of the frozen pond for a distance of about .5 mile. The stand, which is well established and probably much expanded since Hodgdon's 1958 record, is linear; most trees grow within two feet of the water's edge.

Hodgdon also mentioned a report of *Betula nigra* on an island in Pawtuckaway Lake. I collected a specimen from an island within the bounds of Pawtuckaway State Park during the summer of 1986. Eight or ten trees were growing in a low wet area on the island. Several dozen trees were also observed on an adjacent shore line. A specimen from Pawtuckaway Lake has been deposited at NHA.

LITERATURE CITED

HODGDON, A. R. AND STEELE, F. L. 1958. The Woody Plants of New Hampshire. Agricultural Experiment Station Bulletin #447. Univ. of New Hampshire. Durham.

227 MELBOURNE STREET
PORTSMOUTH, NH 03801

RHODORA, Vol. 90, No. 863, 1988

BOOK REVIEW

WHITING, R. E. AND P. M. CATLING. *Orchids of Ontario*. Pp. xii + 169. The CanaColl Foundation, K. W. Neatby Bldg., 1010 Carling Ave., Ottawa, Canada, K1A 0C6. 1986. (Price: $12.95 Canadian).

The immense popular appeal of the Orchidaceae has blessed (or cursed) devotees of the family with a steady stream of both technical and popular books, the quality and significance of which vary almost as greatly as the morphology of their subjects. In this regard it is a real pleasure to find in Whiting and Catling's recent account of Ontario's orchid flora a synthesis of scholarship and utility which promises to place the book in the hands of a general audience of botanists and lovers of natural history.

The strength and desirability of a local flora lies in its author's familiarity with the geographical region covered and in the resulting detail which it is possible to present. In the present case, the term "local," however, needs qualification. Ontario includes an immense area. The vastness of the region is often unappreciated by those south of the international boundary. In terms of United States geography, Ontario stretches from New York City to west of Minneapolis and Kansas City. Extending from Lake Erie to the southern shore of Hudson Bay, Ontario encompasses an area roughly comparable to that of the eastern United States.

Yet the detail is there, with literature citations and field experience even to the level of *forma*. Altogether 60 species, 15 varieties (of 7 species), 21 forms, 5 hybrids, and 3 notomorphs are accepted as documented in the flora. These are treated in detail in the "Commentaries," which, together with keys to the genera and species, make up well over half the book. These individual treatments include, for each species, variety, and hybrid, notes on flower color and flowering time, citation of pertinent literature, and discussions of distribution, ecology, and taxonomic problems. Each treatment is introduced with some general comments which may aid in identification, or point out peculiar features or aspects of the plant's natural history or pattern of occurrence in Ontario. Many recount personal field experience. Notes on forms and notomorphs present in the province are incorporated into the treatments of higher level

taxa. The individual accounts are filled with a great deal of information and often make enjoyable reading.

Most species are illustrated with black and white photographs of good to excellent quality, although a few obviously have suffered in the transfer from color originals. *Calypso bulbosa* var. *americana,* certainly one of the world's most exquisite blossoms, graces the cover in color. In some difficult groups, diagnostic line drawings of flowers and floral parts of actual specimens are provided, and in certain cases series of drawings are employed to illustrate variation within, and differences between, species. I do not recall seeing such presentations in any other floristic work. Altogether the illustrations are very useful and should increase greatly the value of the book outside Ontario.

Two appended sections briefly indicate additional species and infraspecific taxa that may occur in Ontario but have yet to be documented there. A third treats excluded taxa.

The keys are clear and should prove to be quite workable. They vary from diagnostic to, in difficult groups, elaborately descriptive. Possible ambiguities are addressed with parenthetics. The keys coupled with the illustrations and notes in the text and thoroughly up-to-date taxonomy and nomenclature make this a most useful volume for identification, and it should be a first choice for workers throughout eastern and central Canada and the northeastern and midwestern United States.

Distributions are plotted on one or another of three base maps of different scales, these covering progressively smaller portions of the province. Although this variability in maps dictates some mental effort in visual comparisons of ranges of different species, the greater detail possible for species restricted to southern Ontario more than makes up for any inconvenience. Separate maps are provided for each species, variety, and hybrid (forms are not indicated but the notomorphs of *Cypripedium* × *andrewsii* are separately identified on one map), and the dots plot actual localities. While this presents a great deal of data and makes the maps much more meaningful than the more common plotting of counties or some other artificial grid, one wonders whether this practice will not invite destruction of some populations through collection for the garden. This is certainly a problem in some areas. I only hope that the Canadian public is more enlightened than their southern neighbors.

Hopefully countering any possible threat presented by the maps is a rather extensive treatment of orchid rarity, habitat destruction, and protection. The loss of habitat and species is discussed, and two maps graphically document dramatic range reductions. Legal protection, such as it is, is outlined, and, in a particularly important contribution, the authors present lists of species and varieties considered to be in need of protection. These are listed as endangered, threatened, rare, or uncommon. A fifth list includes hybrids and forms. Criteria for inclusion in each list are clearly stated.

Two maps provide a key to counties and districts of Ontario. A discussion of recent changes in political boundaries within the province will be of use to anyone wishing to plot old records on a new base map, or to correlate new and old records. For many, these two features may well be worth the price of the book. Also included are introductory sections on the morphology of orchid flowers and an excellent review of the relevant orchid literature. A handy flowering time chart, glossary, and extensive bibliography complete the volume. Figures, tables, maps, and orchid taxa are thoroughly indexed. This is a very well thought-out book.

Many of us from the vicinity of the Great Lakes, who found in Fred Case's 1964 *Orchids of the Western Great Lakes Region* a guide not only to the region's orchid flora but to a career and a way of life as well, will recognize at last in *Orchids of Ontario* a worthy companion volume.

C. J. SHEVIAK
BIOLOGICAL SURVEY
THE STATE EDUCATION DEPARTMENT
NEW YORK STATE MUSEUM
ALBANY, NY 12230

RHODORA, Vol. 90, No. 863, 1988

BOOK REVIEW

BEAL, ERNEST O. AND JOHN W. THIERET. *Aquatic and Wetland Plants of Kentucky*. 315 pp. Kentucky Nature Preserves Commission. Scientific and Technical Series, Number 5. 1986. Send orders to: Kentucky Nature Preserves Commission, 407 Broadway, Frankfort, Kentucky 40601. (Price: $20.00, paper.)

This book covers the herbaceous vascular plants growing in the aquatic and wetland habitats of Kentucky. The general format consists of keys, generic descriptions, habitat notes, overall range, county-distribution maps, illustrations, glossary, and an extensive literature cited section. The format followed in this book is different from the conventional style. A series of dichotomous keys are utilized to identify the plant to family. At that point all taxa are arranged alphabetically. For example, if one is to key out Cyperaceae, it is listed in the C's and if the plant to be identified keys out to *Fimbristylis,* one then turns to *Fimbristylis* in the F's to key it to species. This makes the format very easy to use.

The illustrations are excellent. Many of the same illustrations were originally used in Beal's *A Manual of Marsh and Aquatic Vascular Plants of North Carolina.* These are simple illustrations, that, in many cases, show just the major diagnostic characters. At the end of the book are county dot maps for Kentucky, which are arranged alphabetically by taxa. The maps have dots for all specimens cited which have a herbarium voucher. Triangles are utilized for literature records. This information is extremely valuable for the taxa that are at the edge of their ranges, especially those at the northeastern end of their ranges.

The easy format and the many illustrations make this an attractive book for the non-botanist. I would highly recommend this book to all that are interested in aquatic plants.

C. BARRE HELLQUIST
DEPARTMENT OF BIOLOGY
NORTH ADAMS STATE COLLEGE
NORTH ADAMS, MASSACHUSETTS 01247

NEBC AWARD
FOR THE SUPPORT OF BOTANICAL RESEARCH

The Awards Committee of the New England Botanical Club is pleased to announce that C. Thomas Philbrick of the University of Connecticut has been selected to be the 1988 award recipient. Mr. Philbrick, who is a graduate student with Dr. Gregory Anderson, submitted a proposal entitled "Systematic Studies in *Callitriche* (Callitrichaceae) in North America."

Awards Committee:
R. Tryon, Chair
A. Bussewitz
B. Hellquist
R. Primack

Vol 90, No. 862, including pages 113–213, was issued April 30, 1988

The New England Botanical Club
22 Divinity Avenue
Cambridge, Mass. 02138

The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 90th year and contains about 500 pages a volume.

Membership is open to all persons interested in systematics and field botany. Annual dues are $25.00, including a subscription to RHODORA. Students may apply for a Student Membership at $10.00 a year, which does not include a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

Regular Member	$25.00
Family Membership	$35.00
Student Member	$10.00
For this calendar year	_____
For the next calendar year	_____

Name _____

Address _____

City & State _____ Zip _____

Special interests (optional):

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8″) **throughout** including tables, figure legends, and literature citations. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

RHODORA July 1988 Vol. 90, No. 863

CONTENTS

A new Pilea (Urticaceae) from Hispaniola
James D. Skean, Jr. and *Walter S. Judd* 215
Description and distribution of Euphrasia stricta in North America
Stephen R. Downie and *John McNeill* 223
Reproductive biology of two sympatric species of Chimaphila
Lisa A. Standley, Sarah S. -H. Kim and *Ingrid M. Hjersted* . . . 233
Taxonomy of Arnica (Asteraceae) subgenus Arctica
Stephen R. Downie and *Keith E. Denford* 245
Taxonomy of Senecio streptanthifolius Greene
John F. Bain 277
A reevaluation of the Triglochin maritimum complex (Juncaginaceae) in eastern and central North America and Europe
Bruce A. Ford and *Peter W. Ball* 313
NEW ENGLAND NOTES
Aster nemoralis is extant in Vermont
Peter F. Zika 339
Kudzu (Pueraria lobata) in New England
Bruce A. Sorrie and *William D. Perkins* 341
Betula nigra at Mendum's Pond, Barrington, NH and Pawtuckaway Lake, Nottingham, NH
Charles R. Cormier 345
BOOK REVIEWS
Orchids of Ontario
Charles Sheviak 347
Aquatic and Wetland Plants of Kentucky
C. Barre Hellquist 351
ANNOUNCEMENT
NEBC Award 352
NEBC Membership Application Form 353
Instructions to Contributors . . . . . inside back cover

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 90 October 1988 No. 864

The New England Botanical Club, Inc.

22 Divinity Avenue, Cambridge, Massachusetts 02138

RHODORA

NORTON H. NICKERSON, Editor-in-Chief

Associate Editors

DAVID S. BARRINGTON
A. LINN BOGLE
DAVID E. BOUFFORD
WILLIAM D. COUNTRYMAN
GARRETT E. CROW
RICHARD A. FRALICK
GERALD J. GASTONY
C. BARRE HELLQUIST
MICHAEL W. LEFOR
ROBERT T. WILCE

ISSN 0035-4902

RHODORA.—Published four times a year, in January, April, July, and October by the New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138. Second Class postage paid at Boston, MA. A journal of botany devoted primarily to the flora of North America. Price $25.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to 22 Divinity Avenue, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related areas, and articles concerned with systematic botany and cytotaxonomy in their broader implications will be considered. Brevity is urged; please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Fifty reprints of each article are supplied free of charge. Authors may arrange with Lexington Press for additional copies. RHODORA assesses page charges.

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

POSTMASTER: Send address changes to RHODORA, 22 Divinity Avenue, Cambridge, MA 02138.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS 02173

Cover Illustration

Eupatorium leucolepis var. *novaeangliae* is an endemic New England taxon restricted to upper margins of sandy-peaty coastal plain ponds. Currently vouchered from 7 ponds in MA and 5 in RI (several historical stations are extirpated), New England Boneset is a candidate for federal listing. The nominate variety occurs from Long Island in NY (very rare) and southern NJ to FL and LA.

Original artwork by Caren Caljouw

Rhodora

(ISSN 0035-4902)

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 90 October 1988 No. 864

EVIDENCE OF PRE-COLUMBIAN *BRASSICA* IN THE NORTHEASTERN UNITED STATES

HEATHER A. JACOBSON, JAMES B. PETERSEN AND DAVID E. PUTNAM

ABSTRACT

The genus *Brassica*, a native of Eurasia, has long been considered to have been introduced to the New World by European settlers around 400 B.P. (years before present). Recent examinations of charred seeds from buried fire hearths at three archaeological sites in central Maine reveal that *Brassica kaber* (DC.) Wheeler (charlock) occurred in the region as early as 8000 B.P., and was abundant and widespread by 2000 B.P. These findings are consistent with those from several other archaeological excavations in the northeastern United States.

Key Words: *Brassica*, palaeobotany, ethnobotany, biogeography, archaeological sites, northeastern United States

INTRODUCTION

The fact that many of the common weedy mustards, rapes, and cabbages (*Brassica*) now present in North America originated in Europe and Asia is well documented in the botanical literature (Fernald, 1950; Gleason and Cronquist, 1963; Kartesz and Kartesz, 1980; Rollins, 1981; Great Plains Flora Association, 1986). Approximately 40 species occur in the Mediterranean region, primarily on chalky soil (Gates, 1950). England is the type locality of *Brassica kaber* (DC.) Wheeler var. *pinnatifida* (Stokes) Wheeler, a common weed today in North America (Wheeler, 1938).

This paper reports findings from recent archaeological studies in Maine, and summarizes earlier studies in Vermont, Massachusetts, and Pennsylvania; all reveal that *Brassica kaber* has been a long-standing component of the vegetation of the northeastern United States. This information has implications for our understanding of the timing of dispersal of this species to the New World, and for the means by which such dispersal was accomplished.

STUDY SITES

Three archaeological sites in central Maine yielded the plant materials of interest (Figure 1). These were the Smith site (69-14) and the Smith's Landing site (69-16) (Petersen and Putnam, 1986), both located on the west bank of the Kennebec River in Concord, Somerset County, and the Sharrow Site (90-2d) (Petersen et al., 1986; Petersen and Putnam, 1987), located on the north bank of the Piscataquis River in Milo, Piscataquis County.

The Smith site extends for approximately 200 meters along a fossil riverbank. Prehistoric cultural remains are preserved in sand and silt alluvium. During excavations, fire hearths and related features were encountered in three strata. Calcined bone, plant macrofossils, and charcoal occurred with an assemblage of terminal

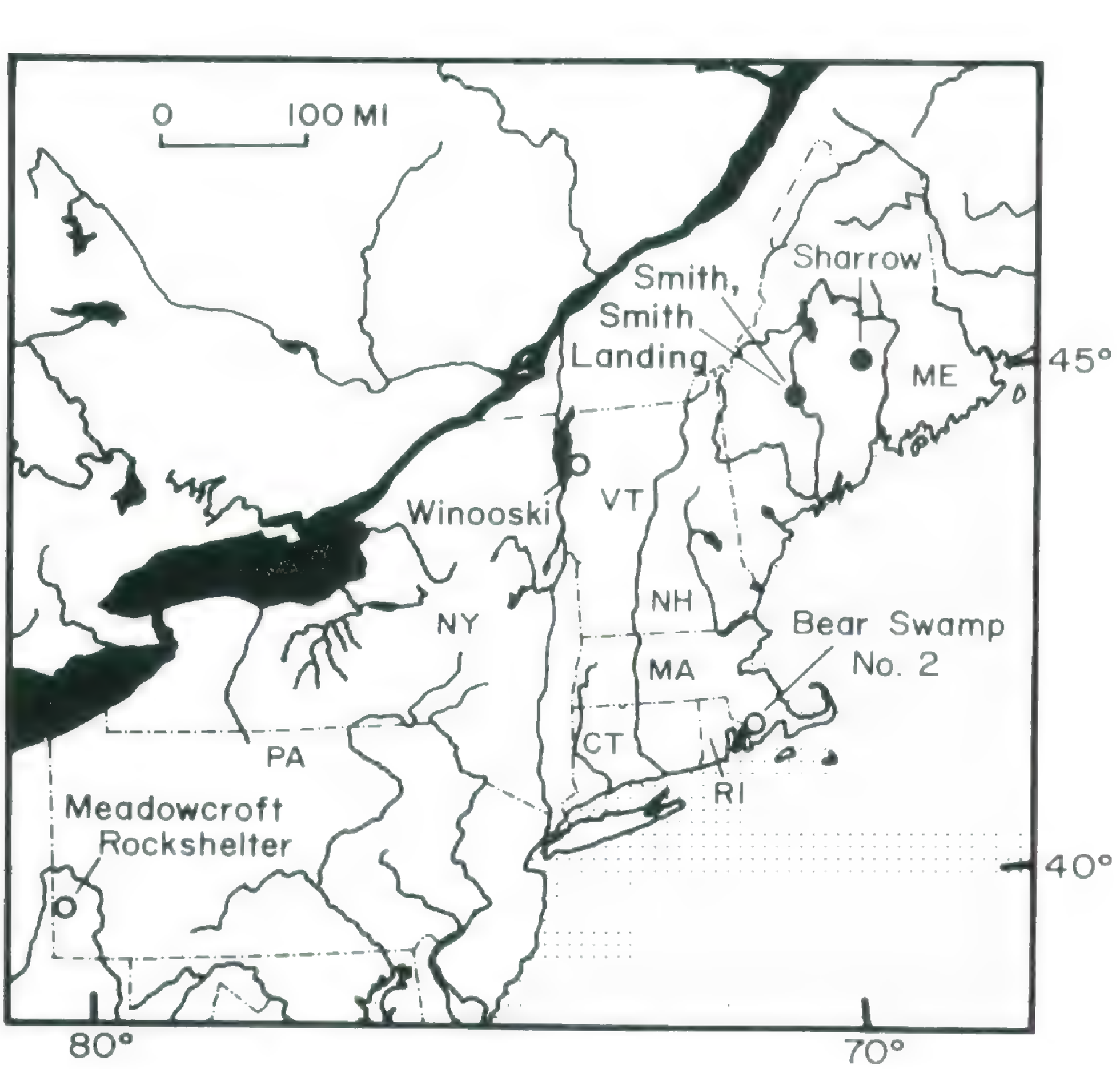


Figure 1. Locations of archaeological sites in the northeastern United States from which *Brassica* seeds were recovered: this study ●; other studies ○.

Archaic artifacts believed to be attributable to the latter end of the Susquehanna tradition, ca. 3,600–2,900 B.P.

The small Smith's Landing site is preserved in ancient sediment that is markedly altered by pedogenesis. The site lacks stratigraphy, but exhibits no evidence of plowing or other historic disturbance. Diagnostic artifacts from several cultural periods were recovered from the site, and *Brassica* seeds were recovered from within a feature in association with a fully grooved, pecked, and ground stone-axe attributable to a Late Archaic period occupation some time ca. 4,500–3,000 B.P.

The Sharrow site is a three-meter-deep stratified sequence of cultural features, the oldest and deepest dating to ca. 9,000 B.P., and the youngest to 1510 ± 80 B.P. Forty-one features (e.g. fire hearths, post holes, etc.) were sampled and processed systematically. Artifacts and radiocarbon dates reveal that they span the past 9,000 years of prehistory.

METHODS

At each of the sites, these fire hearths and other cultural features were completely removed as they appeared in the excavation pits. Feature fill was dry-sieved through a 6.4 mm screen in the field, and through 3.2 mm and 1.0 mm screens in the laboratory using pressurized water. Each fraction of fill was dried, and floral, faunal, and inorganic material was separated under a binocular dissecting microscope. Only charred material recovered from intact features below the plow zone was considered to be prehistoric. Charring increases preservation of plant remains (Minnis, 1981; Dimbleby, 1978), while uncharred material usually degrades rapidly in terrestrial environments. Therefore, uncharred material is considered to be of modern origin and probably intrusive to the features in which it is found. Similarly, charred material not associated with an intact feature is considered to be of unknown original context, and without adequate temporal control.

Both direct and indirect methods were used to date stratigraphic features. Most of the features were dated directly by radiocarbon dating of the feature material itself (e.g., the charcoal in fire hearths). Estimated dates were used in some instances where features occurred between directly dated overlying and underlying features that lay within 10 vertical cm. In addition, cultural artifacts diagnostic of known periods were used as a supplemental check on the dating.

Seeds, capsules, and nut fragments collected from these features were identified under a dissecting microscope at 7× to 30× magnification, using the extensive reference seed collection of the University of Maine's Dept. of Botany and Plant Pathology (MAINE), and the literature (Montgomery, 1977; Landers and Johnson, 1976; Beijerinck, 1947).

Species of *Brassica* can be distinguished on the basis of certain, often subtle, differences in their seeds, including size, shape, color, and surface sculpturing (Musil, 1948). Although burning distorts these characteristics to some degree, the charred specimens could still be confidently identified using Musil's (1948) key and the reference collection. The task of determining *Brassica* species is somewhat simplified in Maine because there are only four species that occur over a broad geographic area: *B. kaber* (DC.) Wheeler var. *pinnatifida* (Stokes) Wheeler, *B. juncea* (L.) Coss., *B. nigra* (L.) Koch, and *B. rapa* L. (Richards et al., 1983). A few other species occur only in coastal areas.

RESULTS AND DISCUSSION

The charred seeds of *Brassica kaber* recovered from the three sites date from ca. 8000–1000 B.P., with the majority of the seeds associated with strata deposited between 4000 and 2000 B.P. (Table 1). These findings raise questions as to what, if any, role this plant played in the lives of native peoples, and how and when the species became a component of North American vegetation.

Association of *Brassica* with Prehistoric Sites

In their comprehensive review of ethnobotanical studies on the historical use of plants for food and medicine by native peoples of eastern Canada, Arnason et al. (1981) reported that young plants of *Brassica* spp., including *Brassica nigra* (L.) Koch (black mustard), were cooked as greens by both the Iroquois and the Malecite Indian tribes. Ground seeds of *Brassica nigra* were used as snuff by the Meskwaki to cure head colds, and the Mohegans used the leaves of this plant to relieve toothaches and headaches (Black, 1980). *Brassica hirta* Moench (white mustard) was used by the Malecite and Micmac to treat tuberculosis, and the bark of *Brassica napus* L. (wild turnip) was used by the Micmac to treat colds, cough, grippe, and small pox (Arnason et al., 1981). Black (1980) reported that the Rappahannock used *B. napus* for chilblains, and *B. oleracea* L. (wild cabbage) for headaches; *B. rapa* L. (bird rape) was also

Table 1. Number of seeds of *Brassica kaber* recovered from separate features at three sites in Maine, with direct (d) and indirect (i) dates.

Location	Sample Age (B.P.)		Seeds per Feature
SMITH SITE			
Concord Twp, Maine	2510 ±60	d	112
	2900 ± 120	d	30
	2930 ± 110	d	113
	3000	i	206, 178, 145.5, 17, 2, 1, 1, 1
	3020 ± 90	d	72
	3090 ± 140	d	24
	3160 ± 80	d	4
	3190 ± 70	d	68
	3200	i	39
	3210 ± 100	d	1
	3350 ± 120	d	38
	3580 ± 100	d	7
SMITH LANDING SITE			
Concord Twp, Maine	4500–3000	i	14, 12
SHARROW SITE			
Milo, Maine	1000	i	14
	2000–1500	i	3
	2500	i	186, 17, 4
	3500	i	2, 2
	3650 ± 110	d	2
	5370 ± 120	d	2
	8250 ± 320	d	2

used as a medicine by the Bois Fort Chippewa. Although *B. kaber* is not mentioned in these ethnographic accounts, its use by native peoples is at least conceivable on the basis of the reviews of Arnason (1981) and Black (1980).

However, *Brassica kaber* is a weedy annual that produces large quantities of seed and flourishes on disturbed ground. *Brassica* seeds could have been merely part of the local seed rain around the occupied site. They could have been haphazardly trapped in the fire hearths and charred in either domestic fires during occupation of the site, or in natural fires after abandonment of the site. The proliferation of weedy annuals on abandoned sites is well documented (Minnis, 1981) and could account for the high numbers of seeds observed (Table 1).

Thus, as Minnis (1981) pointed out, there are three possible sources of these prehistoric seeds: (1) they remained after direct use of the seeds, (2) they remained after use of other parts of the plant,

and (3) they arrived as seed rain unrelated to human use of the plant. In the case of *Brassica kaber*, all three mechanisms are possible.

Geographic and Temporal Distribution of *Brassica*

Seeds of *Brassica* have been recovered from several other archaeological sites in the northeastern United States (Figure 1). Ninety-eight specimens of *Brassica* cf. *kaber* were identified from four loci at the Winooski site in northwestern Vermont (Petersen and Power, 1983). Direct dates on two samples ranged from ca. 1300 800 B.P.; the remaining two samples were dated indirectly to between ca. 1300 1100 B.P. Remains of *Brassica* sp. dated by association to ca. 4450 3950 B.P. were also recovered from the Bear Swamp (No. 2) site in southeastern Massachusetts (Barnes, 1980). Adovasio et al. (1977) reported 10 specimens of *Brassica* sp. remains dating between ca. 3255 925 B.P. from four strata at the Meadowcroft Rockshelter site in southwestern Pennsylvania.

The occurrence of *Brassica* remains in materials from archaeological sites in the northeastern U.S. has important implications for our understanding of the time of introduction and distribution of the genus. Even if we ignore the oldest occurrence of *Brassica* seeds at the Sharrow site, the evidence presented here overwhelmingly suggests that *Brassica kaber* was present in the northeastern United States several thousands of years before European colonization or earlier Viking visits to the New World. If the oldest dates are correct, these Eurasian plants (Fernald, 1950) were already present soon after the widespread colonization of North America by the earliest native Americans who apparently entered from Siberia some time before 11,000 B.P.

It seems unlikely that *Brassica kaber* entered North America through Siberia, however, because the modern semi-circumboreal distribution of the species does not include eastern Asia (Hultén, 1971). A more probable hypothesis is that *Brassica kaber* has maintained a semi-circumboreal distribution during the late-Quaternary, its range within North America changing during glacial/interglacial cycles.

ACKNOWLEDGMENTS

We thank the University of Maine for making the seed collection and laboratory facilities available for this research, C. S. Campbell for helpful discussions, H. Lindstrom of the Ethnobotanical Laboratory at the University of Minnesota for assistance in identifying the

seeds, and G. L. Jacobson Jr. and two anonymous reviewers for their useful suggestions and comments. Archaeological excavations at the Smith and Smith's Landing sites were funded by the Central Maine Power Company. Work at the Sharrow site was funded by the Maine Department of Transportation through the Maine Historic Preservation Commission.

LITERATURE CITED

ADOVASIO, J. M., J. D. GUNN, J. DONAHUE, AND R. STUCKENRATH. 1977. Meadowcroft Rockshelter: a retrospect 1976. Pennsylvania Archaeologist 74 (2 and 3). Society for Pennsylvania Archaeology.

ARNASON, T., R. J. HEBDA, AND T. JOHNS. 1981. Use of plants for food and medicine by Native Peoples of eastern Canada. Canad. J. Bot. 59: 2189–2325.

BARNES, R. C. 1980. Feature analysis: a neglected tool in archaeological survey and interpretation. Man in the Northeast 20: 101 114.

BEIJERINCK, W. 1947. Zadenatlas der Nederlandsche Flora. H. Veenman and Zonen, Wageningen.

BLACK, M. J. 1980. Algonquin ethnobotany: an interpretation of aboriginal adaptation in southwestern Quebec. Canadian Ethology Service Paper 65. National Museum of Man, Mercury Series. Ottawa.

DIMBLEBY, G. 1978. Plants and Archaeology, 2nd ed. Humanities Press. Atlantic Highlands, New Jersey.

FERNALD, M. L. 1950. Gray's Manual of Botany, 8th ed. Reprinted 1970. D. Van Nostrand Co., New York.

GATES, R. R. 1950. Genetics and taxonomy of the cultivated *Brassicas* and their wild relatives. Bull. Torr. Bot. Club 77: 19–28.

GLEASON, H. A., AND A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van. Nostrand Co., Inc. Princeton, N.J.

GREAT PLAINS FLORA ASSOCIATION. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

HULTÉN, E. 1971. The Circumpolar Plants. II. Dicotyledons. Almqvist and Wiksell, Stockholm.

KARTESZ, J. T., AND R. KARTESZ. 1980. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland. University of North Carolina Press, Chapel Hill.

LANDERS, J. L., AND A. S. JOHNSON. 1976. Bobwhite Quail food habits in the southeastern United States with a seed key to important foods. Tall Timbers Research Station, Miscellaneous Publication No. 4, Tallahassee, Florida.

MINNIS, P. E. 1981. Seeds in archaeological sites: sources and some interpretive problems. Amer. Antiquity 46: 143–152.

MONTGOMERY, F. H. 1977. Seeds and Fruits of Plants of Eastern Canada and Northeastern United States. University of Toronto Press, Toronto.

MUSIL, A. F. 1948. Distinguishing the species of *Brassica* by their seed. U.S.D.A. Misc. Publ. No. 643.

PETERSEN, J. B., AND M. W. POWER. 1983. The Winooski Site and the Middle Woodland Period in the Northeast. Report submitted to the Interagency Archaeological Services, Mid-Atlantic Region, National Parks Service, under Contract CX 4000-2-0006.

———, N. D. HAMILTON, D. E. PUTNAM, A. E. SPIESS, R. STUCKENRATH, C. A. THAYER, AND J. A. WOLFORD. 1986. The Piscataquis archaeological project: a Late Pleistocene and Holocene occupational sequence in northern New England. Archaeology of Eastern North America 14: 1–18.

———, AND D. E. PUTNAM. 1986. Archaeological phase II testing in the Williams Hydroelectric Dam increased pool area, Somerset County, Maine. Report prepared for the Central Maine Power Company, Augusta, Maine.

———, AND ———. 1987. Another Holocene sequence and recent progress of the Piscataquis Archaeological Project in central Maine. Curr. Research in the Pleistocene 4: 23–24.

RICHARDS, C. D., F. HYLAND, AND L. M. EASTMAN. 1983. Revised Checklist of the Vascular Plants of Maine. Bull. Josselyn Bot. Soc. Maine. No. 11.

ROLLINS, R. C. 1981. Weeds of the Cruciferae (Brassicaceae) in North America. J. Arnold Arbor. 62: 517-540.

WHEELER, L. C. 1938. The names of three species of *Brassica*. Rhodora 40: 306–309.

H. A. J.
DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF MAINE
ORONO, MAINE 04469

J. B. P. AND D. E. P.
ARCHAEOLOGY RESEARCH CENTER
UNIVERSITY OF MAINE AT FARMINGTON
FARMINGTON, MAINE 04938

RHODORA, Vol. 90, No. 864, 1988

MORPHOLOGICAL VARIABILITY OF A *SCENEDESMUS DENTICULATUS* LAGERH. ISOLATE IN CULTURE AND SOME TAXONOMIC REVISIONS

MASON G. FENWICK

ABSTRACT

The validity of the taxon *Scenedesmus smithii* Teil. and others is questioned. A strain of *S. denticulatus* Lagerh. was grown in cultures and variability observed. Forms were identified in these cultures which could be identified with published taxa: *S. smithii* Teil., *S. denticulatus* var. *fenestrata* (Teil.) Uherkov., *S. denticulatus* Lagerh. f. *crassispinosus* Hortob & Németh, and *S. arcuatus* f. *spinosus* Hortob. & Németh. *Scenedesmus denticulatus* plants from the Fox and Rock Rivers of Illinois are illustrated.

Key Words: *Scenedesmus,* variability, morphology, single culture, taxonomic synonymies

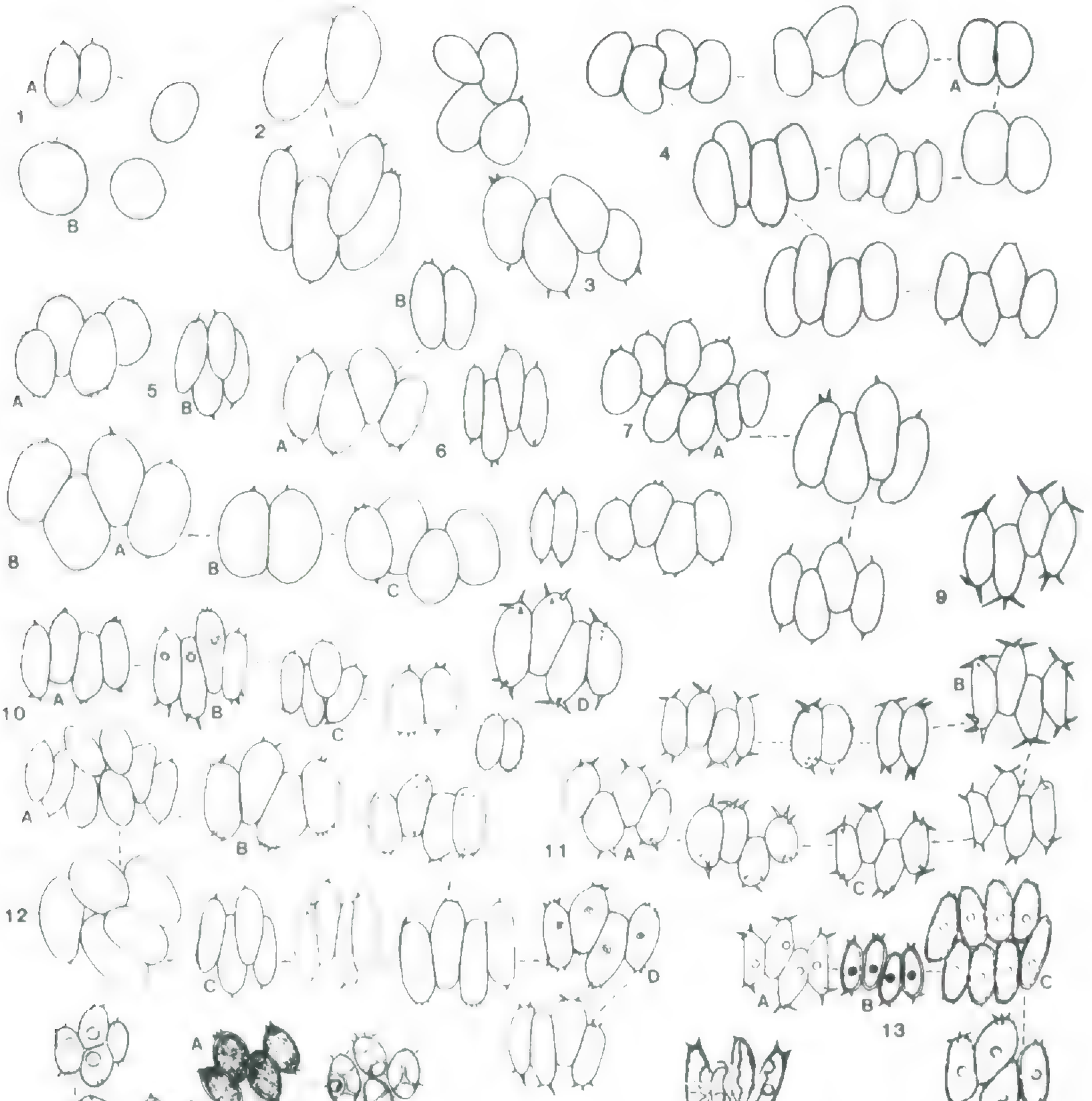
INTRODUCTION

Pleomorphism of *Scenedesmus* and the taxomic difficulties encountered are well known. Several authors who have studied morphological variability in this genus include Chodat (1926), Trainor et al. (1963, 1967, 1971, 1974, 1979), Komárek and Ludvik (1972), Hindák (1974), Hegewald (1982), and Comas and Komárek (1984). We have experienced difficulty in defining the taxa *S. denticulatus* and *S. smithii* and have grown a strain of *S. denticulatus* in various media to determine the extent of its pleomorphism. From this study we find that the plants illustrated in the literature as *S. smithii* are probably natural variants of the taxon *S. denticulatus* Lagerh.

METHODS

An isolate of a strain identified as *Scenedesmus denticulatus*[1] was cultured. The alga was grown on substrates similar to those we used in the investigation of pleomorphism in the genus *Coelastrum* (Fenwick et al., 1966; Lynch et al., 1967). The substrates are listed in

[1]Culture 19.81, identified as *S. denticulatus* Lager'h. Hegewald, No. 1976/56. Pflanzenphysiologisches Institute der Universität Göttingen. Nikolausberger Weg 18, D. 3400, Göttingen.


A
1
B
2
3
4
A
5
A
B
B
6
A
7
A
8
B
A
B
C
9
10
A
B
C
D
11
A
C
B
12
C
D
13
A
B
C
D
14
A
15
16
17
18
19
20
21
22
23
24
10 µm
Figs. 1–12, 17–24

the key to Figures 1–12 of Plate 1. Regarding the other illustrations, Figures 13–16 are reproduced from Komárek and Fott (19834, Pl. 233), and Figures 17–24 are this author's drawings of plants from the Fox and Rock Rivers.

RESULTS

Ahlstrom (1934; unpubl. Ph.D. dissertation, Ohio State Univ.) in his monograph recognized the variability of *Scenedesmus denticulatus* as indicated by his description of the taxon which follows: "It has unusual colonial arrangements: 2-celled individuals are linear, 4-celled are subalternate and 8-celled colonies are radiate in form. Four-celled colonies are seldom flat. Cells are variable in shape, being oblong, ovoid, or irregularly cylindrical. They are also variable in proportion of length to width. This species is armed with 1 to 5 spines (usually 2 to 3) of varying length. The inner cells have spines on the free poles only. Ahlstrom's figure (1934, Pl. 1, Figure 11) of the taxon closely resembles the plants in our cultures shown in Figures 12B, 11A. Coenobia shown in our Figure 14 (from Komárek and Fott, 1983, Pl. 233, Figure 8) show Lagerheim's iconographs (first 3 figures) of *S. denticulatus*, the last 2 figures Hortobágy's (1967).

Plants interpreted as *Scenedesmus smithii* by Teiling (1942), iconotype reproduced in Figure 13A (from Komárek and Fott, 1983), seem to be identical to forms of *S. denticulatus* obtained in culture (*see* Figures 9, 11B, and 11C). Other Coenobia which have been designated as *S. smithii* in literature, shown in Figures 13B, C, D, are from Philipose (1967), Komárek (1983) and Bourrelly (1966) respectively. Komárek (1983) stated that the *S. smithii* he described from Cuba (reproduced in Figure 13C) differs from the similar *S.*

Figures 1–12 represent the *Scenedesmus denticulatus* isolate cultured in various media. **1.** Plants grown on Bold's Basal Medium agar. **2–7. 12.** Plants grown in BBM plus an organic carbon source added at 10g/liter concentration: **2.** BBM + casein; **3.** BBM + sucrose; **4.** BBM + galactose; **5.** BBM + mannitol; **6.** BBM + glucose; **7.** BBM + starch; **12.** BBM + maltose. **8–11.** Plants grown in other substrates: **8.** 4% soil extract; **9.** BBM solution; **10.** BBM + soil extract; **11.** soil extract enriched with bean cotyledon and calcium (Stein, 1973, p. 22). Figures **13–16** are reproduced from Komárek and Fott (1983, pl. 233, figures 5–7), with permission of Dr. Komárek: **13.** Plants published as *S. smithii* Teil; **14.** Published figures of *S. denticulatus* Lagerh.; **15.** *S. denticulatus* f. *crassispinosus* Hortob. and Németh. Figures **17–20, 23, 24** are forms of *S. denticulatus* from the Fox River, early summer. **21.** Plant collected under ice in the Fox River. **22.** Plant from the Rock River in late summer.

denticulatus by having narrower elliptical cells which are gathered more densely in the coenobium. This cell shape and arrangement seem to be a normal variation of *S. denticulatus* seen in culture (Figures 10–12).

Bourrelly and Couté (1986, Pl. V, Figure 3) illustrated a plant from Reunion as *Scenedesmus smithii* that appears to be identical to a plant from a culture of *S. denticulatus* (Figure 11E). Both thickness and length of spines are variable features as indicated in our cultures (*see* Figures 5, 6, 11, 12). The *S. denticulatus* f. *crassispinosus* of Hortobágyi and Németh (1963) with the thick spines, probably an ecoform, is similar to our larger-spined forms. These same authors also described a plant from the same fish pond as *S. arcuatus* f. *spinosus;* it resembles some of our plants which were grown in organically enriched media (Figures 2–8). Uherkovich's (1966, Pl. 6, Figure 213) *S. denticulatus* var. *fenestratus* (Teil.) Uherk., originally named *S. fenestratus* by Teiling (1942), looks like one of the variants seen in culture (Figure 7A). A similar coenobium (Figure 19) was collected from the Fox River.

Scenedesmus denticulatus plants collected from the Fox River are shown in Figures 17–21, 23, 24 and from the Rock River in Figure 22. Large 8-celled coenobia (Figures 20, 24) observed from the Fox River were not present in our cultures. Smith (1926, Pl. 17, Figures 19, 22) designated these as *S. denticulatus* as well as forms similar to our Figure 11 from culture. Granules that were scarcely visible occurred on the lateral walls of cells of some coenobia in our cultures (Figures 12, 18). Plants having well-defined granules have been recorded by Hortobágyi as *S. denticulatus* f. *granulatus* Hartob. (1969) and by Hegewald (1976).

CONCLUSION

Based on this study, the names of published taxa of *Scenedesmus smithii* Teil. *S. denticulatus* var. *fenestratus* (Teil.) Uherkov., *S. denticulatus* f. *crassispinosus* Hortob. & Németh, and *S. arcuatus* f. *spinosus* Hortob. & Németh are considered to be synonyms of *S. denticulatus* Lagerh.

LITERATURE CITED

Bourrelly, P. 1966. Les alques d'eau douce. 1. Les algues vertes. 1st. ed.

_____ and Couté. 1986. Algues d'douce de l'ile de la Réunion (Diatomees exclues). Cryptogamie, Algologie 7: 87–121.

CHODAT, R. 1926. *Scenedesmus.* Étude de génétique de systematique expérimentale et d'Hydrobiologie. Schweiz. Z. Hydrol. 3(3, 4): 71–258.

COMAS, A. AND J. KOMÁREK. 1984. Taxonomy and nomenclature of several species of *Scenedesmus* (Chlorellales). Arch. Hydrobiol. Suppl. 67, Algological Studies 135–157.

FENWICK, M. G., L. O. HANSEN AND D. L. LYNCH. 1966. Polymorphic forms of *Coelastrum proboscideum* Bohl. Trans. Amer. Microscop. Soc. 85: 579–581.

HEGEWALD, E. 1976. A contribution to the algal flora of Jamaica. Nova Hedwigia 28: 45–69.

_____. 1982. Taxonomische morphologische untersuchung von *Scenedesmus* Isolaten aus Stammsammlungen. Arch. Hydrobiol. Suppl. 60, 4. Algological Studies 29: 375–406.

HINDÁK, F. 1974. The morphological variability of *Scenedesmus pannonicus* Hortob. in culture. Arch. Hydrobiol. Suppl. 46, Algological Studies 11: 130–139.

HORTOBÁGYI, T. 1969. Algen aus Vietnam IV. Acta Bot. Acad. Sci. Hung. 15(1–2): 37–69.

_____ AND T. NÉMETH. 1963. Neue Algen aus den Fischteichen von Gödöllo. Acta Bot. Acad. Sci. Hung. 9(3–4): 307–321.

KOMÁREK, J. 1983. Contribution to the Chlorococcal algae of Cuba. Nova Hedwigia 37: 65–180.

_____ AND B. FOTT. 1983. Chlorococcales. *In:* Huber-Pestalozzi, Da Phytoplankton des Süsswassers, Systematik und Biologie, 7 Teil, Stuttgart.

_____ AND J. LUDVIG. 1972. Die Zellwandultrastrukture als taxonomishes Merkmal in der Gattung *Scenedesmus.* Arch. Hydrol. Biol. Suppl. 41, Algological Studies 6, 11–47.

LAGERHEIM, G. 1882. Bitrãg till kännedomen om Stockholmstrakens Pediastreer, Protococcacéer och Palmellacéer. [Ein Beitrag zur Kenntnis der pediastraceen, Protococcaceen und Palmellaceen in dem Gebiet von Stockholm.] Öfv. Kgl. Vetensk. Akad. Förh. Stockholm, 1882: 47–81.

LYNCH, D. L., M. G. FENWICK, L. O. HANSEN. 1967. Heterotrophic nutrition in the genus *Coelastrum* Naeg. Trans. Amer. Microscop. Soc. 86: 499–502.

PHILIPOSE, M. T. 1967. Chlorococcales. I.C.A.R. New Delhi.

PRESCOTT, G. W. 1962. Algae of the western Great Lakes area. Wm. C. Brown Co., Inc., Dubuque, Iowa.

SMITH, G. W. 1926. The plankton algae of the Okobogi region. Trans. Amer. Microscop. Soc. 45: 156–233.

STEIN, J. R. 1973. Handbook of Phycological Methods. Cambridge University Press.

TEILING, E. 1942. Schwedische Planktonalgen 3. Neue oder wenig bekannte Formen. Bot. Notiser, Lund 1942: 63–68.

TRAINOR, F. R., J. R. CAIN, AND L. E. SHUBERT. 1976. Morphology and nutrition of the colonial alga *Scenedesmus:* 80 years later. Bot. Rev. 42: 5–25.

_____, AND R. L. HILTON, JR. 1963. Culture of *Scenedesmus longus.* Bull. Torrey Bot. Club 90: 407–412.

_____ AND F. G. ROSKOSKY. 1967. Spine pattern in several clones of a *Scenedesmus.* Trans. Amer. Microsop. Soc. 86: 16–21.

———, H. L. Rowland, J. C. Lylis, P. A. Winter, and P. L. Bonanom. 1971. Some examples of polymorphism in algae. Phycologia 10: 113–119.
——— and L. E. Shubert. 1974. *Scenedesmus* morphogenesis. Colony control in dilute media. J. Phycol. 10: 28–30.
Uherkovich, G. 1966. Die *Scenedesmus* - Arten Ungarns. Budapest.

DEPARTMENT OF BIOLOGICAL SCIENCES
NORTHERN ILLINOIS UNIVERSITY
DEKALB, IL 60115
USA

RHODORA, Vol. 90, No. 864, 1988

NEW AND NOTEWORTHY PLANT RECORDS FOR MINNESOTA

GERALD B. OWNBEY AND WELBY R. SMITH

ABSTRACT

First Minnesota records or confirmation of older records for the following angiosperms are reported: *Ruellia humilis, Asclepias hirtella, Asclepias stenophylla, Aster pilosus, Shinnersoseris rostrata, Solidago ×bernardii, Draba norvegica, Butomus umbellatus, Polanisia jamesii, Paronychia fastigiata, Commelina erecta, Sedum integrifolium, Eleocharis rostellata, Myriophyllum spicatum, Hamamelis virginiana, Scutellaria parvula, Utricularia resupinata, Allium cernuum, Sphaeralcea coccinea, Coralorrhiza odontorhiza, Poa paludigena, Spartina gracilis, Dodecatheon media, Lysimachia quadrifolia, Saxifraga cernua,* and *Viola nuttallii.* Phytogeographical and historical information supplementing these reports is also given. Specimens upon which the reports are based are cited.

Key Words: plant records, range extensions, rare plant information, new records, plant geography, Minnesota

INTRODUCTION

Extensive plant collecting in Minnesota, particularly during the past ten years, has added much new information on the rare plants of the state. Some of the most significant range extensions and new records for the state are recorded herewith. All cited specimens are or shortly will be deposited in MIN.

ACANTHACEAE

Ruellia humilis Nutt.

The range of this species given by Long (1961) included Minnesota, but no specimen was cited. It is not listed for Minnesota in the regional manuals, nor has a specimen been seen in Minnesota herbaria. The specimen cited here represents a significant northern range extension of about 150 miles from Crawford Co., Wisconsin (Read, 1976).

Washington Co.: T28N, R20W, sect. 34, SE 1/4, SE 1/4, Afton State Park, Aug. 29, 1974, *Forester, s.n.*

ASCLEPIADACEAE

Asclepias hirtella (Pennell) Woodson

This species was reported for Minnesota by Woodson (1954), but

no specimen was cited and we have located no specimen in Minnesota herbaria. The site reported here was discovered by Mr. Jack Heather of Rochester, MN.

Mower Co.: T101N, R14W, sect. 5, NE 1/4, NW 1/4, Cartney State Wildlife Management Area, July 29, 1982, *Smith 6951*.

Asclepias stenophylla Gray

The Minnesota locality for this species is widely disjunct from its Great Plains distributional area shown in the Atlas of the Flora of the Great Plains (Barkley, 1977). Nearest records shown in the atlas are in eastern Nebraska. The small Minnesota population occupies the southwestern corner of a precipitous river bluff and is associated with other prairie species.

Houston Co.: T104N, R5W, sect. 34, SW 1/4, 3.6 mi. W of Hokah, June 19, 1976, *Ownbey 5187;* same locality, Aug. 14, 1978, *Ownbey 6138*.

ASTERACEAE

Aster pilosus Willd.

This widespread *Aster* was first collected in Minnesota in 1914 insofar as MIN records indicate, and was not re-collected until 1973. It was not included by Rosendahl and Cronquist (1949) in their treatment of the asters of Minnesota, although Fernald (1950) included the state in his generalized distribution of the species.

Winona Co.: Winona Bluff Side Park, Oct., 1914, *Holzinger, s.n.* Olmsted Co: 1.5 mi. S, 1 mi. E of Chester, Oct. 6, 1973, *Neese, s.n.*; same locality, Sept. 25, 1974, *Ownbey 4881*. Rice Co.: T110N, R20W, sect. 20, Trout Lily Preserve, Sept. 10, 1982, *Galatowitsch 779*.

Shinnersoseris rostrata (Gray) Tomb

This Great Plains species is found naturally in Minnesota only at the Agassiz Dunes, Norman and Polk counties. A recent collection from Sherburne Co. undoubtedly is an introduction from Great Plains seed sources, brought in during a prairie restoration project. Outside Minnesota, the nearest locality mapped by Tomb (1973) is in southeastern North Dakota.

Norman Co.: T146N, R44W, sect. 18, SE 1/4, NE 1/4, July 17, 1985, *Dana 85058*. Polk Co.: Agassiz Dunes Natural Area, 1 mi. S, 0.5 mi. W of Fertile, July 13, 1974, *Ownbey 4805*.

Solidago ×**bernardii** Boivin [*S. ptarmicoides* (Nees) Boivin × *S. riddellii* Frank]

This hybrid may be expected to occur wherever the parental species grow in proximity.

Becker Co.: T142N, R43W, sect. 16, SW 1/4, NE 1/4, Zimmerman Prairie, 10 mi. W of Ogema, Aug. 12, 1980, *Severson 708*. Clay Co.: T141N, R45W, sect. 5, NE 1/4, Blazing Star Prairie, 4 mi. SE of Felton, Aug. 29, 1979, *Ottoson 122;* S of Buffalo State Park, Aug. 15, 1962, *Stevens 2621*. Mahnomen Co.: T145N, R41W, sect. 6, 7, Santee Prairie, 3 mi. SE of Bejou, Aug. 7, 1979, *Herman 153*. Norman Co.: T143N, R45W, sect. 23, SW 1/4, Twin Valley Prairie, 5 mi. W of Syre, Aug. 29, 1979, *Herman 194*. Polk Co.: T149N, R45W, sect. 8, S 1/2, Pankratz Prairie North, 7 mi. SE of Crookston, Aug. 15, 1979, *Farrel 217*.

BRASSICACEAE

Draba norvegica Gunner

A small colony of this northern species was discovered on Susie Island, Cook Co., MN, in 1937 (Butters and Abbe, 1953). To the best of our knowledge, this is the only locality for the species in the United States to the present time. Recently, after an interval of 43 years, the population was re-located and today consists of only a few individuals.

Cook Co.: T63N, R7E, sect. 5, NW 1/4, SW 1/4, Susie Island in Lake Superior, June 22, 1980, *Smith 2586*.

BUTOMACEAE

Butomus umbellatus L.

This introduced Eurasian plant has the potential for spreading through the waterways of Minnesota. So far it is known from only two localities.

Rice Co.: In standing water of ditch at Cannon Lake along Hwy. 60, June 24, 1972, *Sutherland, Parker & Kaul 3198*. Becker Co.: West Lake Drive, Detroit Lakes, July 10, 1976, *Long, s.n.*

CAPPARACEAE

Polanisia jamesii (T. & G.) Iltis

The natural distribution of this species as shown in the Atlas of the Flora of the Great Plains (Barkley, 1977) extends to eastern Nebraska in the central plains. Isolated localities are shown by Iltis (1958) in eastern Iowa, central and northwestern Illinois and northwestern Wisconsin. It is known in Minnesota from a single locality where it is flourishing but it does not appear to be spreading.

Dakota Co.: T114N, R17W, sect. 11, NE 1/4, sand dune area 2 mi. SE of Hastings, July 26, 1978, *Ownbey 6073*.

CARYOPHYLLACEAE

Paronychia fastigiata (Raf.) Fern.

The specimens cited are the first collections of this species from Minnesota at MIN. A collection made by J. M. Holzinger in 1897 from Trempealeau Mt. is from Wisconsin, not from Winona Co., Minnesota, as is inferred by the label. The Holzinger collection may be the basis for the inclusion of Minnesota in the distribution of *P. fastigiata* by Fernald (1950).

Washington Co.: T28N, R20W, sect. 14, SW 1/4, SW 1/4, 0.5 mi. N of Afton village near mouth of Valley Creek, Sept. 3, 1976, *Ownbey 5491;* T28N, R20W, sect. 35, NE 1/4, SW 1/4, Afton State Park, July 26, 1981, *Ownbey 6699.*

COMMELINACEAE

Commelina erecta L.

This, the first Minnesota record for the species, is disjunct approximately 120 miles from the nearest location given by Read (1976) in Sauk Co., Wisconsin.

Wabasha Co.: T109N, R9W, sect. 5, SW 1/4, SE 1/4, Aug. 13, 1983, *Galatowitsch 885.*

CRASSULACEAE

Sedum integrifolium (Raf.) Nels. subsp. **leedyi** (Rosend. & Moore) Clausen

This taxon was discovered in Olmsted Co., MN, in 1936 and described initially as *Sedum rosea* (L.) Scop. var. *leedyi* Rosend. & Moore (Rosendahl and Moore, 1947). It was believed to exist only at the type locality until Clausen (1975) determined that a population in New York state was consubspecific with the Minnesota plants. He also transferred the taxon to *S. integrifolium.* The type locality in Minnesota still supports a large population. Reported herewith are two additional Minnesota populations recently located in an adjacent county by the junior author and Dr. Terry Frest.

Fillmore Co.: T103N, R13W, sect. 13, NW 1/4, NE 1/4, NW 1/4, 4 mi. W-NW of Wykoff, May 15, 1985, *Smith 10072;* T103N, R12W, sect. 6, NW 1/4, SW 1/4, NE 1/4, 1.5 mi. SE of Washington, May 15, 1985, *Smith 10096.*

CYPERACEAE

Eleocharis rostellata Torr.

This species was reported by Glaser (1983) from a single locality in Minnesota. Subsequent collections indicated it occurs more

widely in the state. These records fill a major gap in the known distribution of this transcontinental species. It apparently is limited to habitats associated with calcareous or circumneutral fens.

Becker Co.: T142N, R42W, sect. 13, NE 1/4, NE 1/4, Spring Creek State Wildlife Management Area, July 18, 1982, *Smith 6795.* Clearwater Co.: T149N, R37W, sect. 17, NW 1/4, SW 1/4, Aug. 6, 1982, *Smith 7105.* Koochiching Co.: T152N, R29W, sect. 3, NW 1/4, SW 1/4, July 17, 1983, *Smith 8344.* Mahnomen Co.: T143N, R42W, sect. 25, SW 1/4, NW 1/4, Waubun State Wildlife Management Area, July 14, 1982, *Smith 6730.* Scott Co.: T115N, R21W, sect. 17, NW 1/4, SE 1/4, Savage Fen, July 15, 1987, *Smith 13510.*

HALORAGACEAE

Myriophyllum spicatum L.

This introduced Eurasian and African aquatic weed was not reported for Minnesota by Couch and Nelson (1985) in their exhaustive study of its distribution in North America. The identity of the cited specimen was verified by Dr. Susan Aiken.

Hennepin Co.: along the S shore of Excelsior Bay in Lake Minnetonka, Sept. 9, 1987, *Pennings, s.n.*

HAMAMELIDACEAE

Hamamelis virginiana L.

The Witch-Hazel has been known from southeastern Minnesota for many years, and its presence in Minnesota to the north in the St. Croix River drainage has been postulated but not confirmed until recently.

Chisago Co.: Camp Waubojeeg, ca. 2 mi. N of Taylor's Falls city limit on Hwy. 15, W side of road near top of St. Croix valley wall, Aug. 10, 1986, Crawford, *s.n.*

LAMIACEAE

Scutellaria parvula Michx.

The only Minnesota specimen of *Scutellaria parvula*, in the strict sense, seen by the authors is cited below. All other specimens from the state are *S. leonardi* Epling or, when treated as a variety, *S. parvula* var. *leonardi* (Epling) Fern.

Washington Co.: Railroad right-of-way, 2.5 mi. NE of the town of Point Douglas, June 4, 1937, *Moore & Moore 10020.*

LENTIBULARIACEAE

Utricularia resupinata Greene

These are the first Minnesota records of the species known to the

authors. They are approximately 100 miles from the nearest site at Thunder Bay, Ontario (Scoggan, 1978) and about the same distance from sites in northern Wisconsin.

Lake Co.: T63N, R7W, sect. 12, NW 1/4, NW 1/4, Bow Lake, Aug. 13, 1984, *Knowles, s.n.* (DUL); T64N, R6W, sect. 23, SW 1/4, SE 1/4, Makwa Lake, Aug. 19, 1987, *Smith 13888;* T64N, R6W, sect. 34, NE 1/4, NW 1/4, Pan Lake, Aug. 19, 1987, *Smith 13898.*

LILIACEAE

Allium cernuum Roth

Although previously reported from Minnesota (Barkley, 1977; Gleason and Cronquist, 1963), no authentic specimen from the state was located during our search of Minnesota herbaria. Because this species is frequently confused with *Allium stellatum* Ker, we are somewhat skeptical of previous reports. The Minnesota record reported herewith is consistent with authentic records (MIN) from the southern tier of counties in Wisconsin and from Allamakee Co., Iowa.

Mower Co.: T101N, R14W, sect. 21, SW 1/4, SW 1/4, Lake Louise State Park, July 30, 1982, *Smith 7018.*

MALVACEAE

Sphaeralcea coccinea (Nutt.) Rydb.

This species was discovered in Minnesota by Mr. John Schladweiler of New Ulm, MN, who showed the site to the junior author. The species is common in the Great Plains (Barkley, 1977), and the Minnesota locality represents a range extension of perhaps 50 miles from Day Co., South Dakota.

Lac Qui Parle Co.: T117N, R46W, sect. 5, SE 1/4, SE 1/4, Salt Lake State Wildlife Management Area, May 20, 1987, *Smith 12736.*

ORCHIDACEAE

Coralorrhiza odontorhiza (Willd.) Nutt.

First collected in Minnesota by C. O. Rosendahl in 1899, this species was not collected again until 1979.

Goodhue Co.: T112N, R13W, sect. 6, SE 1/4, SE 1/4, 3 mi. NW of Frontenac, Aug. 28, 1979, *Smith 1598;* T112N, R13W, sect. 22, SW 1/4, NW 1/4, about 5 mi. NW of Lake City, Sept. 24, 1984, *Smith 9967.* Hennepin Co.: T120N, R22W, sect. 34, SE 1/4, SW 1/4, NW 1/4, Eastman Nature Center, Oct. 11, 1982, *Smith 7625;* T118N, R23W, sect. 27, NE 1/4, SW 1/4, NW 1/4, Wolsfeld Woods Scientific and Natural Area, Oct. 3, 1982, *Smith 7623.* Houston Co.: Spring Grove, Aug., 1899, *Rosendahl 1158.* Wabasha Co.: T109N, R9W, sect. 7, 8, Weaver Dunes, Sept. 6,

1982, *Galatowitsch 750*. Washington Co.: 0.5 mi. WNW of Afton, Oct. 7, 1979, *Ownbey 6560*. Wright Co.: T121N, R27W, sect. 5, SE 1/4, SW 1/4, about 1/8 mi. S of Bass Lake, Sept. 5, 1982, *Smith 7558;* T122N, R26W, sect. 30, SW 1/4, SW 1/4, Hoglund State Wildlife Management Area, about 5.5 mi. SSE of Clearwater, Sept. 24, 1982, *Smith 7615*.

POACEAE

Poa paludigena Fern. & Wieg.

We know of no earlier Minnesota records for this rare swamp species. It previously is known from adjacent portions of Wisconsin and Iowa, as well as several eastern states.

Pine Co.: T41N, R20W, sect. 23, NW 1/4, SW 1/4, Kettle River Natural Area, June 9, 1980, *Converse 208;* T38N, R20W, sect. 21, NE 1/4, SW 1/4, Kettle River State Scientific and Natural Area, June 18, 1987, *Smith 13006*. Washington Co.: T31N, R19W, sect. 19, NE 1/4, NW 1/4, June 9, 1982, *Smith 12862*.

Spartina gracilis Trin.

These, the first Minnesota records of *Spartina gracilis*, represent a range extension of perhaps 50 miles from the previously reported stations in North Dakota (Barkley, 1977).

Clay Co.: T139N, R46W, sect. 15, SW 1/4, SW 1/4, Bluestem Prairie, July 22, 1980, *Severson 545*. Norman Co.: T144N, R45W, sect. 33, NW 1/4, W 1/2, July 30, 1985, *Dana 85085*. Wilkin Co.: T133N, R45W, sect. 24, NE 1/4, SE 1/4, NW 1/4, Foxhome Prairie, Aug. 17, 1981, *Benson 371*.

PRIMULACEAE

Dodecatheon media L.

This is the first Minnesota record of this eastern and midwestern species. It was previously known from Howard Co., Iowa, ca. 20 miles south of the Minnesota state line. The site reported here was long known to local garden club members, and was brought to the attention of the junior author by Ms. Kathy Bolin of Rochester, MN.

Mower Co.: T101N, R15W, sect. 24, NW 1/4, SW 1/4, LeRoy, Oct. 22, 1980. *Smith 3718*.

Lysimachia quadrifolia L.

This widespread eastern and midwestern species previously has not been reported from Minnesota. The record represents a westward range extension from adjacent Wisconsin where it is common.

Pine Co.: T41N, R17W, sect. 33, SE 1/4, NW 1/4, St. Croix Natural Area, June 24, 1980, *Converse 388*.

SAXIFRAGACEAE

Saxifraga cernua L.

The only midwestern site for this arctic-alpine species was discovered by Butters and Abbe (1953) in Cook Co., MN, in 1930. They re-collected the site in 1937, but it was not visited again until 1980 when about a dozen plants were located at the original spot.

Cook Co.: T65N, R2E, sect. 13, SW 1/4, SW 1/4, Mountain Lake, Aug. 23, 1980, *Coffin & Engstrom 22.*

VIOLACEAE

Viola nuttallii Pursh

Viola nuttallii was reported for Minnesota by Gleason and Cronquist (1963), but not by Fernald (1950), Barkley (1977), or Russell (1966). Despite the Gleason and Cronquist report, the presence of the species in the state remained in doubt until it was discovered by Ms. Micki Buer of Madison, MN, who showed the site to the junior author. The records reported here extend the eastern periphery of the species range by approximately 50 miles from Roberts Co., South Dakota (Barkley, 1977).

Lac Qui Parle Co.: T116N, R45W, sect. 27, NE 1/4, SW 1/4, Antelope Hills, May 8, 1982, *Smith 5875;* T119N, R46W, sect. 33, SE 1/4, S 1/2, Nassau, May 8, 1982, *Smith 5887.*

LITERATURE CITED

BARKLEY, T. M., ED. 1977. Atlas of the Flora of the Great Plains. The Iowa State University Press, Ames.

BUTTERS, F. K. AND E. C. ABBE. 1953. A floristic study of Cook County, northeastern Minnesota. Rhodora 55: 21–55; 63–101; 116–154; 161–201.

CLAUSEN, R. T. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell Univ. Press, Ithaca.

COUCH, R. AND E. NELSON. 1985. *Myriophyllum spicatum* in North America. Proc. of the first International Symposium on Watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Vancouver, B.C.

FERNALD, M. L. 1950. Gray's Manual of Botany, 8th ed., corrected printing, 1970. D. Van Nostrand Co., New York.

GLASER, P. H. 1983. *Eleocharis rostellata* and its relation to spring fens in Minnesota. Michigan Bot. 22: 19–21.

GLEASON, H. A. AND A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand Reinhold Co., New York.

ILTIS, H. H. 1958. Studies in Capparidaceae–IV. *Polanisia* Raf. Brittonia 10: 33–58.

LONG, R. W. 1961. Convergent patterns of variation in *Ruellia caroliniensis* and *R. humilis* (Acanthaceae). Bull. Torrey Bot. Club 88: 387–396.

READ, R. H. 1976. Endangered and threatened vascular plants in Wisconsin. Wisconsin Dept. of Natural Resources Tech. Bull. 92, Madison.

ROSENDAHL, C. O. AND A. CRONQUIST. 1949. The asters of Minnesota: a floristic study. Amer. Midl. Naturalist 42: 502–512.

———, AND J. W. MOORE. 1947. A new variety of *Sedum rosea* from southeastern Minnesota and additional notes on the flora of the region. Rhodora 49: 197–202.

RUSSELL, N. H. 1966. Violets (*Viola*) of central and eastern United States: an introductory survey. Sida 2: 1–113.

SCOGGAN, H. J. 1978. The Flora of Canada. National Museum of Natural Sciences, Publications in Botany No. 7. National Museums of Canada, Ottawa.

TOMB, A. S. 1973. *Shinnersoseris*, gen. nov. (Compositae: Cichorieae). Sida 5: 183-189.

WOODSON, R. E. 1954. The North American species of *Asclepias* L. Ann. Missouri Bot. Gard. 41: 1–201.

G. B. O.
DEPT. OF BOTANY
UNIVERSITY OF MINNESOTA
ST. PAUL, MN 55108

W. R. S.
MINNESOTA DEPARTMENT OF NATURAL RESOURCES
500 LAFAYETTE ROAD
ST. PAUL, MN 55146

RHODORA, Vol. 90, No. 864, 1988

FRESHWATER DIATOMS (BACILLARIOPHYCEAE) FROM THE NORTHEASTERN GLACIAL LAKE DISTRICT OF WISCONSIN. II. *CYMBELLONITZSCHIA*, *HANTZSCHIA*, AND *NITZSCHIA* (ORDER PENNALES, FAMILY NITZSCHIACEAE).

LOUIS L. LIPSEY, JR[1]

ABSTRACT

Twenty-six species and subspecific taxa within the pennate diatom genera *Cymbellonitzschia* Hust., *Hantzschia* Grun., and *Nitzschia* Hass. are described from the Highland Lake District of northeastern Wisconsin. Line drawings, occasional morphological comments, and general information on their distribution within the lake district are also provided.

Key Words: algae, diatoms, Bacillariophyceae, Pennales, Nitzschiaceae, Wisconsin

INTRODUCTION

Diatoms with apical and/or transapical symmetry and whose structural center is normally formed by a line belong to the Order Pennales. Simonsen (1979) recognized two Suborders, the Araphidineae and the Raphidineae (valves without and with a raphe), respectively.

Taxa belonging to the Family Nitzschiaceae characteristically possess a fully developed raphe on a keel, usually subtended by fibulae, at or near the valve margin. Although the family contains eleven genera (Simonsen, 1979), only *Cymbellonitzschia* Hust., *Hantzschia* Grun., and *Nitzschia* Hass. have been recorded from northeastern Wisconsin. Species and subspecific taxa within these genera are treated here. Terminology describing the position of the raphe within the Nitzschiaceae conforms to the definitions of Schoeman and Archibald (1976). Otherwise the general format follows that of the first paper in this series (Lipsey, 1987).

[1]Address for correspondence: 507 Oak Ave., Aurora, IL, 60506.

SYSTEMATIC TREATMENT OF THE SPECIES

Division Chrysophyta
Class Bacillariophyceae
Order Pennales
Family Nitzschiaceae

The separation of *Hantzschia* and *Nitzschia* on the basis of their symmetry has been highly controversial (Schütt, 1896; Karston, 1928; Mann, 1977). However, the transferral of *Hantzschia fenestrata* to *Nitzschia hierosolymitana* "...means that *Hantzschia* can still be identified by the property that its cells are always hantzschioid in symmetry..." (Mann, 1980, p. 259).

KEY TO THE GENERA

1. Valves semi-circular ..... *Cymbellonitzschia*
1. Valves elliptic, lanceolate, linear-lanceolate, or linear 2
2. Valves with directly opposite keels (= hantzschioid symmetry); valve outlines asymmetrical with respect to the apical plane ..... *Hantzschia*
2. Valves with diagonally opposite keels (= nitzschioid symmetry); valve outlines symmetrical with respect to the apical plane ..... *Nitzschia*

CYMBELLONITZSCHIA Hust.

Vegetative cells usually solitary. Valves semi-elliptic, with rounded apices; striae transverse; usually with an elevated keel extending along the ventral margin; fibulae distinct; raphe branches concealed. Valves rectangular in girdle view, generally rhombic in cross-section; raphe-bearing keels directly opposite each other.

C. diluviana Hustedt, 1954. (Figure 3).

DESCRIPTION: Valves semi-circular, 10–16 μm long and 3μm wide; apices rounded; striae finely punctate, parallel, usually 22 24 per 10 μm; keel marginal; fibulae 7.5–8.4 per 10 μm.

IRON CO: Third Black Lake. ONEIDA CO: Minocqua and Pelican Lakes. VILAS CO: Big Sand, Eagle, and North Twin Lakes.

HANTZSCHIA Grun.

Vegetative cells usually solitary. Valves linear, slightly falcate, longitudinally asymmetrical, with rostrate to capitate apices; striae transverse; usually with an elevated keel extending along the incurved margin; fibulae distinct, generally with a distinct central

nodule; raphe branches concealed. Valves rectangular in girdle view, usually rectangular in cross-section; raphe-bearing keels directly opposite each other.

KEY TO THE TAXA

1. Valves 226–344 μm in length; striae 12–14 per 10 μm. .... **3.** *H. elongata*
1. Valves 33–136 μm in length; striae usually more than 15 per 10 μm ..... 2.
2. Valves with rostrate apices .... **1.** *H. amphioxys* var. *amphioxys*
2. Valves with very slender, slightly capitate, apices .... **2.** *H. amphioxys* var. *vivax*

1. **H. amphioxys** (Ehrenb.) Grun. var. **amphioxys** *In:* Cleve and Grunow, 1880. (Figure 1).

DESCRIPTION: Valves linear, slightly falcate, 33–76 μm long and 6–8.5 μm wide; apices rostrate, slightly recurved; striae parallel at the center of the valve, becoming convergent toward the apices, 15–22 per 10 μm; keel marginal, usually with a conspicuous central nodule; fibulae robust, 5–7.1 per 10 μm.

FOREST CO: Deep Hole and Rice Lakes. IRON CO: Trude Lake. ONEIDA CO: Spirit Lake. VILAS CO: Big Sand, Diamond, Eagle, North Twin, and Tippecanoe Lakes.

2. **H. amphioxys** var. **vivax** (Hantz.) Grun. *In:* Cleve and Grunow, 1880. (Figure 2).

DESCRIPTION: Valves linear, slightly falcate, 68–136 μm long and 8–10 μm wide; apices usually very slender, slightly capitate; striae parallel at the center of the valve, becoming convergent toward the apices, 16–18 per 10 μm; keel marginal, usually with a conspicuous central nodule; fibulae robust, 5.5–8 per 10 μm

ONEIDA CO: Spirit, Virgin, and Whitefish Lakes.

3. **H. elongata** (Hantz.) Grun. *In:* Cleve and Grunow, 1880. (Figure 34).

DESCRIPTION: Valves linear, slightly falcate, 226–344 μm long and 12–13.5 μm wide; apices slender, usually capitate; striae parallel at the center of the valve, becoming slightly convergent toward the apices, 12–14 per 10 μm; keel marginal, usually with a conspicuous central nodule; fibulae 5–6 per 10 μm.

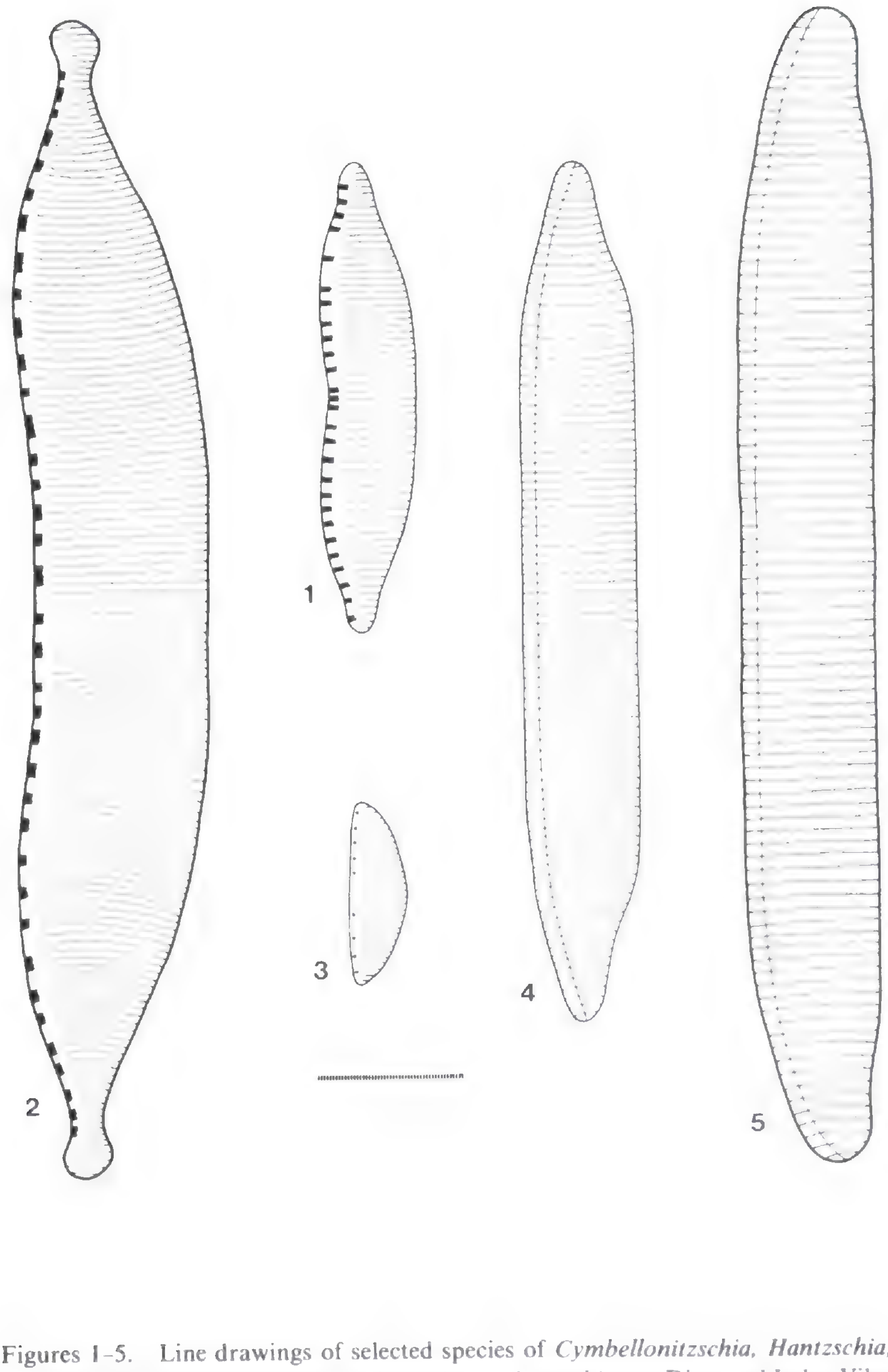
IRON CO: Long Lake. ONEIDA CO: Spirit Lake. VILAS CO: Black Oak and McCullough Lakes.

NITZSCHIA Hass.

Vegetative cells usually solitary. Valves elliptic, linear, or linear-lanceolate, longitudinally asymmetrical, with rounded, rostrate, or capitate apices; striae transverse; generally with an elevated keel extending along one margin; fibulae distinct, at times with a distinct central nodule; raphe branches concealed. Valves rectangular in girdle view, usually rhombic in cross-section; raphe-bearing keels diagonally opposite each other.

KEY TO TAXA

1. Valves with longitudinal folds ..... 2.
1. Valves without longitudinal folds ..... 4.
2. Fibulae distinct, about 6 per 10 μm ..... **21.** *N. tryblionella*
2. Fibulae indistinct ..... 3.
3. Valves with obtusely rounded apices. ..... **3.** *N. angustata* var. *angustata*
3. Valves with protracted, acutely rounded, apices ..... **4.** *N. angustata* var. *acuta*
4. Frustules distinctly sigmoid in girdle view. . **18.** *N. sigmoidea*
4. Frustules not distinctly sigmoid in girdle view ..... 5.
5. Fibulae costa-like, extending about half-way into the center of the valve ..... 6.
5. Fibulae not costa-like, not extending about half-way into the center of the valve ..... 8.
6. Margin of valve with raphe-bearing keel slightly sinuate in outline ..... 7.
6. Margin of valve with raphe-bearing keel not sinuate in outline ..... **5.** *N. denticula*
7. Valves with broadly inflated central margins; striae ca. 18 per 10 μm ..... **20.** *N. sinuata* var. *tabellaria*
7. Valves without broadly inflated margins; striae 23–26 per 10 μm ..... **19.** *N. sinuata* var. *delognei*
8. Valves with a central or slightly excentric keel 9
8. Valves usually with a marginal keel..... 10.
9. Margins of valve centrally constricted and slightly undulate..... ..... **7.** *N. dissipata* f. *undulata*
9. Margins of valve parallel or mildly inflated .... **6.** *N. dissipata* var. *dissipata*
10. Apices of valve usually long and needle-like. . . **1.** *N. acicularis*
10. Apices of valve usually not needle-like ..... 11.



Figures 1–5. Line drawings of selected species of *Cymbellonitzschia, Hantzschia,* and *Nitzschia* from northeastern Wisconsin. **1.** *H. amphioxys,* Diamond Lake, Vilas Co.; **2.** *H. amphioxys* var. *vivax,* Virgin Lake, Oneida Co.; **3.** *C. diluviana,* Third Black Lake, Iron Co.; **4.** *N. angustata* var. *acuta,* Spirit Lake, Oneida Co.; **5.** *N. angustata,* Little Tomahawk Lake, Oneida Co. (Scale bar = 10 μm.)

11. Frustules with centrally constricted margins ....**13.** *N. linearis*
11. Frustules with parallel margins ..... 12.
12. Valves with very fine, usually unresolvable, striae ..... 13.
12. Valves with evident striae ..... 17.
13. Fibulae 6–7 per 10 μm; valves narrowing to acutely rounded apices .....**16.** *N. recta*
13. Fibulae usually more than 6–7 per 10 μm; valves with capitate apices ..... 14.
14. Fibulae spaced more widely apart in the center; margins with raphe-bearing keel at times slightly constricted .... **10.** *N. gandersheimiensis*
14. Fibulae equidistant throughout; margins with raphe-bearing keel usually not constricted ..... 15.
15. Valve width 1/7–1/11 the length ..... **14.** *N. palea* var. *palea*
15. Valve width usually less than 1/11 the length ..... 16.
16. Fibulae 8.4–11 per 10 μm .....**12.** *N. intermedia*
16. Fibulae 12–17.6 per 10 μm .... **15.** *N. palea* var. *tenuirostris*
17. Striae 12.5–19 per 10 μm ..... 18.
17. Striae 24–32 per 10 μm ..... 20.
18. Valves 8–13 μm in length; striae indistinctly punctate ....**22.** *N. valdestriata*
18. Valves 13–53 μm in length; striae distinctly punctate.....19.
19. Valve width 1/9.4–1/10.6 the length; valve apices slightly capitate ..... **11.** *N. hollerupensis*
19. Valve width 1/3.4–1/5.4 the length; valve apices generally rounded .....**2.** *N. amphibia*
20. Valves narrowly lanceolate ..... **17.** *N. romana*
20. Valves lanceolate to linear-lanceolate ..... 21.
21. Margins of valve usually inflated; valve apices usually protracted and acutely rounded ..... **8.** *N. fonticola*
21. Margins of valve usually parallel or slightly incurved; valve apices usually cuneate-rounded..... **9.** *N. frustulum*

Figures 6–15. Line drawings of selected species of *Nitzschia* from northeastern Wisconsin. **6.** *N. romana,* Horsehead Lake, Oneida Co.; **7.** *N. romana,* Clear Lake, Iron Co.; **8.** *N. frustulum,* Clara Lake, Lincoln Co.; **9.** *N. frustulum,* Long Lake, Langlade Co.; **10.** *N. fonticola,* Duck Lake, Langlade Co.; **11.** *N. frustulum,* Duck Lake, Langlade Co.; **12.** *N. palea,* Bug Lake, Forest Co.; **13.** *N. palea,* Lake-of-the-Falls, Iron Co.; **14.** *N. palea,* Clara Lake, Lincoln Co.; **15.** *N. palea* var. *tenuirostris,* Ground Hemlock Lake, Forest Co. (Scale bar = 10 μm.)

6

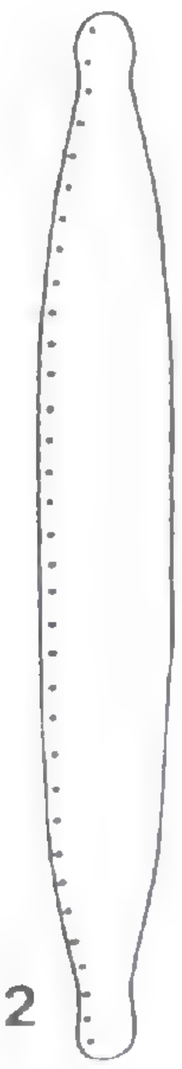
7

8

9

10

11


12

13

14

15

1. **N. acicularis** (Kütz.) W. Smith, 1853. (Figure 24).

DESCRIPTION: Valves narrowly lanceolate, 60–111 μm long and 2–4.5 μm wide; apices very slender, needle-like; striae finely punctate, scarcely visible under LM; keel marginal, usually without a conspicuous central nodule; fibulae 15.3–17 per 10 μm.

COMMENTS: Schoeman (1970) emended the description of this taxon and illustrated its morphological variability. Valve lengths of ca. 20 μm have been reported by Tynni (1980, pl. 12, fig. 188).

IRON CO: Echo Lake. ONEIDA CO: Bearskin, Crescent, Horsehead, and Whitefish Lakes. PRICE CO: Duroy, Long, and Pike Lakes. VILAS CO: Crab and North Twin Lakes.

2. **N. amphibia** Grunow, 1862. (Figures 19–20).

DESCRIPTION: Valves linear to linear-lanceolate, 13–27 μm long and 4–5 μm wide; apices obtusely rounded, occasionally cuneate; striae punctate, parallel, 15–16 per 10 μm; keel marginal, usually without a conspicuous central nodule; fibulae 5.9–9 per 10 μm.

COMMENTS: Hustedt (1922, *In:* A. Schmidt, figs. 34–47) and Schoeman et al. (1984, figs. 72–86) have shown that this species may exhibit a high degree of variability.

FOREST CO: Ground Hemlock, Metonga, and Richardson Lakes. IRON CO: Long, Lower Springstead, Pine, Tank, Trude, and Turtle-Flambeau Lakes; and Lake-of-the-Falls. LANGLADE CO: Long Lake. ONEIDA CO: Bearskin, Crescent, Katherine, Minocqua, Nokomis, North Two, Pelican, Spirit, Squash, Venus, Virgin, and Whitefish Lakes. VILAS CO: Big Arbor Vitae, Big Sand, Black Oak, Catfish, Crab, Deadman, Flambeau, McCullough, North Twin, Palmer, Rice, and Upper Gresham Lakes.

3. **N. angustata** (W. Sm.) Grun. var. **angustata** *In:* Cleve and Grunow, 1880. (Figure 5).

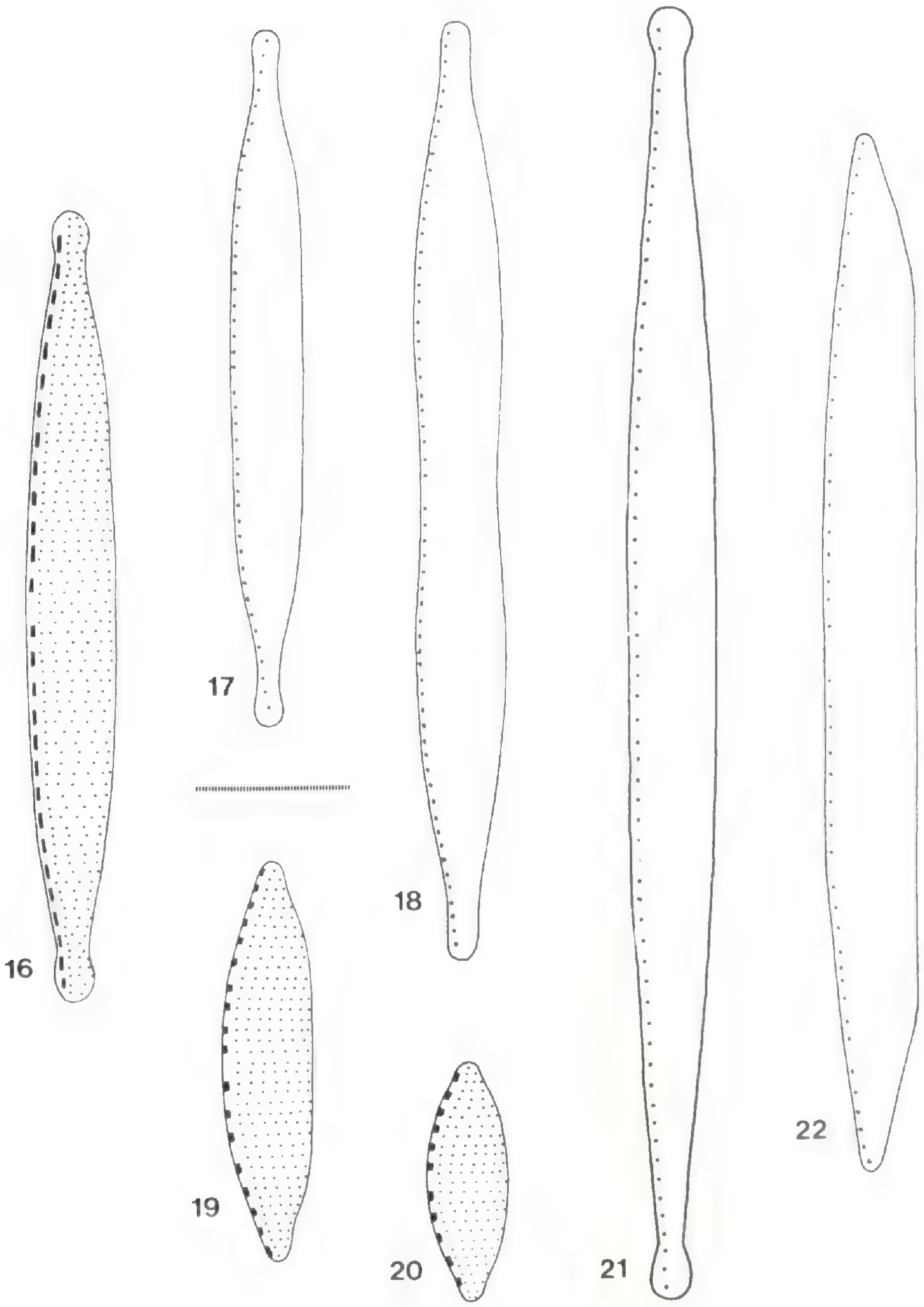
DESCRIPTION: Valves linear, 79–101 μm long and 8.5–9 μm wide; apices obtusely rounded, slightly rostrate; striae indistinctly punctate, parallel, generally 11–12 per 10 μm; keel marginal, usually without a conspicuous central nodule; fibulae indistinct.

FOREST CO: Ground Hemlock Lake. ONEIDA CO: Little Tomahawk Lake.

4. **N. angustata** var. **acuta** Grun. *In:* Cleve and Grunow, 1880. (Figure 4).

DESCRIPTION: Valves linear to linear-lanceolate, 43–64 μm long and 7–8 μm wide; apices protracted, acutely rounded; striae indistinctly punctate, parallel, 14–15 per 10 μm; keel marginal, usually without a conspicuous central nodule; fibulae indistinct.

ONEIDA CO: Spirit and Squash Lakes. VILAS CO: Big Sand, Black Oak, Crab, and Star Lakes.



Figures 16–22. Line drawings of selected taxa of *Nitzschia* from northeastern Wisconsin. **16.** *N. hollerupensis,* Spirit Lake, Oneida Co.; **17.** *N. gandersheimiensis,* Rice Lake, Forest Co.; **18.** *N. gandersheimiensis,* Long Lake, Iron Co.; **19.** *N. amphibia,* Crescent Lake, Oneida Co.; **20.** *N. amphibia,* Ground Hemlock Lake, Forest Co.; **21.** *N. intermedia,* Wabikon Lake, Forest Co.; **22.** *N. recta,* Silver Lake, Forest Co. (Scale bar = 10 μm.)

5. **N. denticula** Grun. *In:* Cleve and Grunow, 1880. (Figure 23).

DESCRIPTION: Valves lanceolate, 18–43 μm long and 5–7 μm wide; apices rounded, occasionally subrostrate; striae punctate, parallel, 14–18 per 10 μm; keel marginal, without a conspicuous central nodule; fibulae costa-like, usually extending nearly half-way into the center of the valve, about 5–6.4 per 10 μm.

COMMENTS: Schoeman and Ashton (1982) have illustrated the morphological variability of this species from samples collected in agricultural waters in the vicinity of the Pretoria Salt Pan (Republic of South Africa).

FOREST CO: Himley and Wabikon Lakes. IRON CO: Clear, Pine, and Trude Lakes. LINCOLN CO: Harrison Lake. ONEIDA CO: Katherine, Squash, and Virgin Lakes. VILAS CO: Big, Big Arbor Vitae, Flambeau, Palmer, Spider, Star, and Upper Gresham Lakes.

6. **N. dissipata** (Kütz.) Grun var. **dissipata** *In:* Cleve and Grunow, 1880. (Figure 26).

DESCRIPTION: Valves linear to linear-lanceolate, 28–125 μm long and 3–7 μm wide; apices rostrate to capitate; striae finely punctate, scarcely visible under LM; keel central to excentric, usually without a conspicuous central nodule; fibulae robust, 4.8–10 per 10μm.

FOREST CO: Ground Hemlock, Himley, and Rice Lakes. IRON CO: Long and Third Black Lakes. LINCOLN CO: Pine Lake. ONEIDA CO: Crescent, Horsehead, Monocqua, Sand, Squash, and Whitefish Lakes. PRICE CO: Butternut, Duroy, and Pike Lakes. VILAS CO: Big Arbor Vitae, Big Sand, Black Oak, Crab, Fence, Flambeau, and North Twin Lakes; and Lac-du-Lune and Lac Vieux Desert.

7. **N. dissipata** f. **undulata** Sovereign, 1963. (Figure 25).

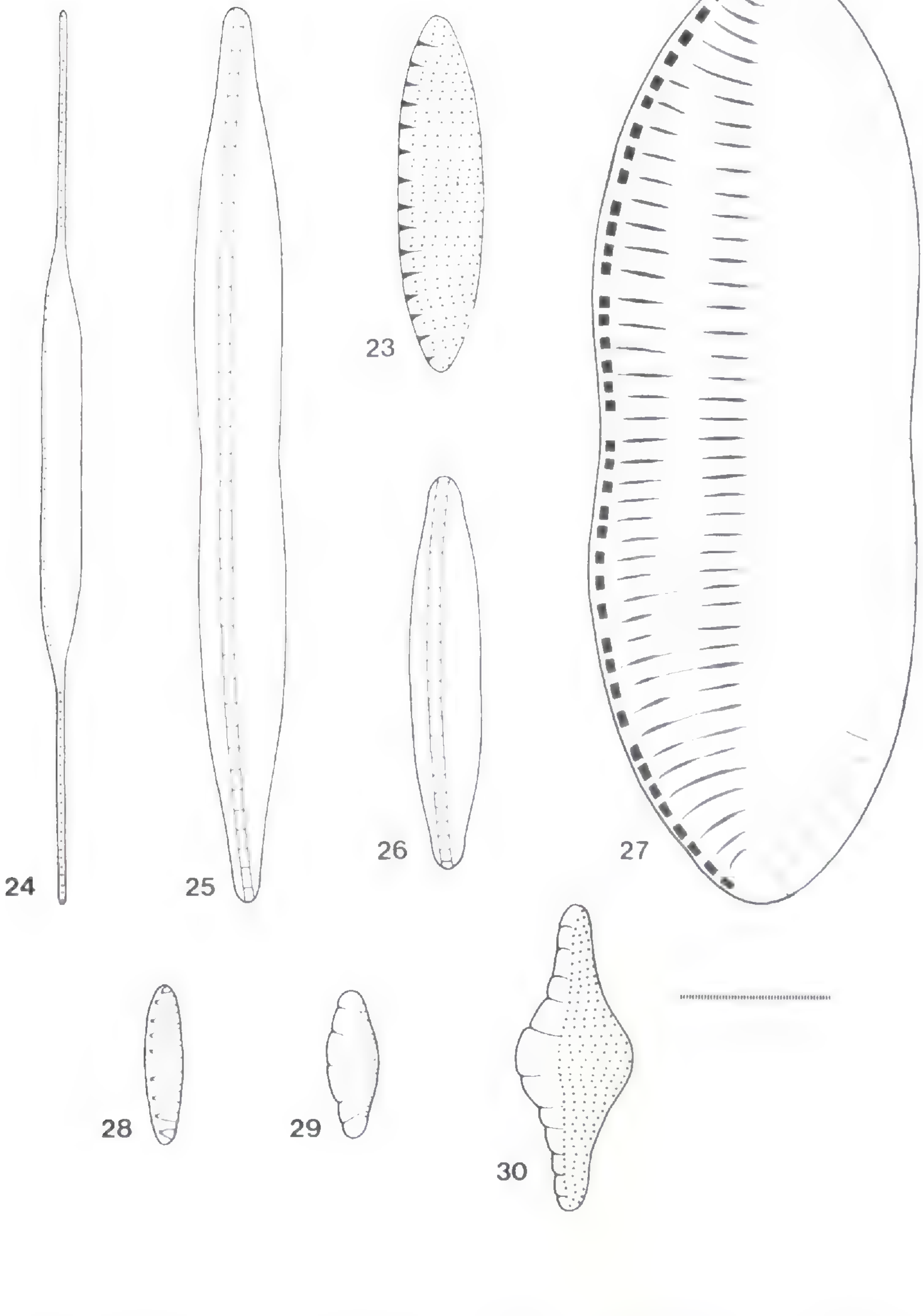
DESCRIPTION: Valves linear to linear-lanceolate, 55–63.5 μm long and 4–5.5 μm wide, with undulate margins; apices rostrate to capitate; striae finely punctate, scarcely visible under LM; keel central to excentric, usually without a conspicuous central nodule; fibulae robust, 5.6–7.1 per 10 μm.

IRON CO: Echo and Turtle-Flambeau Lakes. VILAS CO: Crab Lake.

8. **N. fonticola** Grun. *In:* Van Heurck, 1881. (Figure 10).

DESCRIPTION: Valves lanceolate, 11–18 μm long and 3.5–4.5 μm wide; apices protracted, acutely rounded; striae indistinctly punctate, parallel, 24–28 per 10 μm; keel marginal, usually without a conspicuous central nodule; fibulae 8.5–10 per 10 μm.

LANGLADE CO: Duck Lake. ONEIDA CO: Dorothy, Spirit, Venus, and Virgin Lakes. VILAS CO: Big Gibson, Big Muskellunge, Big Sand, and Black Oak Lakes.



Figures 23–30. Line drawings of selected species of *Nitzschia* from northeastern Wisconsin. **23.** *N. denticula,* Clear Lake, Iron Co.; **24.** *N. acicularis,* Echo Lake, Iron Co.; **25.** *N. dissipata* f. *undulata,* Echo Lake, Iron Co.; **26.** *N. dissipata,* Minocqua Lake, Oneida Co.; **27.** *N. tryblionella,* Duroy Lake, Price Co.; **28.** *N. valdestriata,* Katherine Lake, Oneida Co.; **29.** *N. sinuata* var. *delognei,* Mercer Lake, Iron Co.; **30.** *N. sinuata* var. *tabellaria,* Nokomis Lake, Oneida Co. (Scale bar = 10 μm.)

9. **N. frustulum** (Kütz.) Grun. *In:* Cleve and Grunow, 1880. (Figures 8–9, 11).

DESCRIPTION: Valves linear to linear-lanceolate, 11 43 μm long and 2.5–4 μm wide, frequently incurved along one margin; apices rounded, sometimes cuneate; striae often indistinctly punctate, parallel, 24–30 per 10 μm; keel marginal, usually with a distinct central nodule; fibulae 5.9–11.9 per 10 μm.

COMMENTS: The two central-most fibulae in this species are distinctly spaced due to the presence of a central nodule (Lange-Bertalot and Simonsen, 1978). Hustedt (*In:* A. Schmidt, 1924) initially illustrated the variability of this taxon. Reimer (1953 54) later reduced *N. hantzschiana* Rabh. and *N. frustulum* var. *minutula* Grun. to synonyms of *N. frustulum,* and emended the description.

FOREST CO: Little Sand, Metonga, Richardson, and Silver Lakes. IRON CO: Feely, Lower Springstead, Mercer, Tank, and Trude Lakes. LANGLADE CO: Duck and Long Lakes. LINCOLN CO: Clara, Half Moon, Harrison, and Pine Lakes. ONEIDA CO: Bearskin, Dorothy, Horsehead, Katherine, Little Bearskin, Minocqua, North Two, Rainbow, Spirit, Squash, Venus, Virgin, Washburn, and Whitefish Lakes. PRICE CO: Butternut and Duroy Lakes. VILAS CO: Big Muskellunge, Big Sand, Black Oak, Catfish, Crab, Eagle, Fence, Flambeau, Ike Walton, McCullough, North Twin, Rice, Spider, and Star Lakes; and Lac-du-Lune and Lac Vieux Desert.

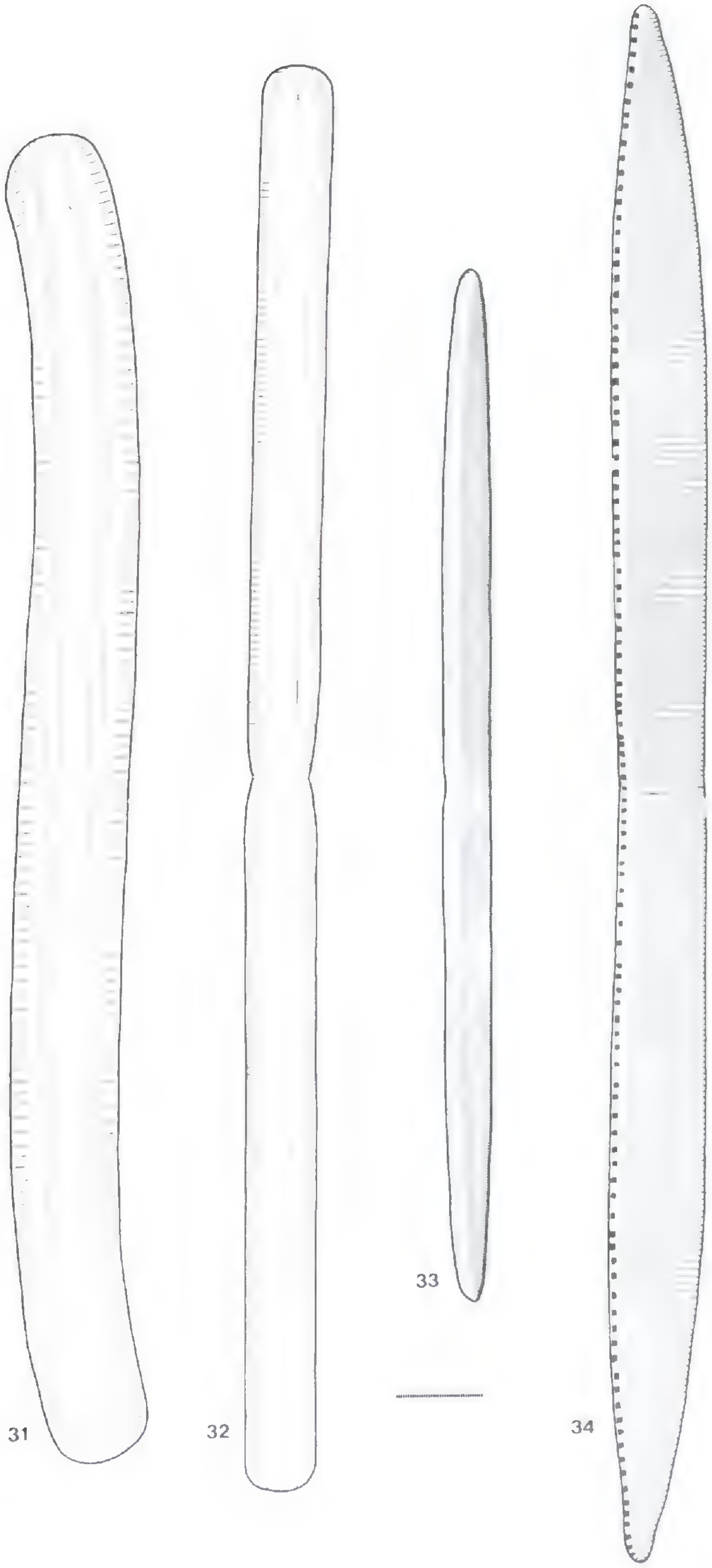
10. **N. gandersheimiensis** Krasske, 1927. (Figures 17 18).

DESCRIPTION: Valves linear-lanceolate to lanceolate, 21 72 μm long and 3 6.5 μm wide, frequently with incurved margins; apices protracted, usually capitate; striae finely punctate, scarcely visible under LM; keel marginal, usually with a distinct central nodule; fibulae 8.9–12.4 per 10 μm.

COMMENTS: This species is extremely variable morphologically. Although conspicuous striae have been observed in *Nitzschia gandersheimiensis* (Lange-Bertalot and Simonsen, 1978), all Wisconsin specimens observed to date characteristically have unresolvable striae.

FOREST CO: Rice Lake. IRON CO: Long and Mirror Lakes; and Lake-of-the-Falls. ONEIDA CO: Bearskin, Crescent, Katherine, Nokomis, North Two, and Pelican Lakes. PRICE CO: Duroy Lake. VILAS CO: Crab, Diamond, and Rice Lakes; and Lac Vieux Desert.

Figures 31-34. Line drawings of selected species of *Hantzschia* and *Nitzschia* from northeastern Wisconsin. **31.** *N. sigmoidea* (girdle view), Lake-of-the-Falls, Iron Co.; **32.** *N. linearis* (girdle view), Himley Lake, Forest Co.; **33.** *N. linearis,* Himley Lake, Forest Co.; **34.** *H. elongata,* Black Oak Lake, Vilas Co. (Scale bar = 10 μm).


31
32
33
34

11. **N. hollerupensis** Foged, 1962. (Figure 16).

DESCRIPTION: Valves linear-lanceolate to lanceolate, 47–53 μm long and ca. 5 μm wide; apices subcapitate; striae distinctly punctate, parallel, 16–19 per 10 μm; keel marginal, usually with a conspicuous central nodule; fibulae 5.5–8.9 per 10 μm.

ONEIDA CO: Spirit and Squash Lakes. VILAS CO: Big Sand and Black Oak Lakes.

12. **N. intermedia** Hantz. *ex* Cleve and Grunow, 1880. (Figure 21).

DESCRIPTION: Valves usually linear to linear-lanceolate, 54–146 μm long and 3 7 μm wide; apices generally narrow, capitate; striae finely punctate, scarcely visible under LM; keel marginal, usually without a conspicuous central nodule; fibulae 8.4–11 per 10 μm.

COMMENTS: Like most other species of *Nitzschia, N. intermedia* is highly variable morphologically. Lange-Bertalot (1977) illustrates several specimens with conspicuous striae. However, all Wisconsin specimens observed thus far have inconspicuous striae.

FOREST CO: Himley, Lucerne, and Wabikon Lakes. IRON CO: Clear Lake. LINCOLN CO: Dudley and Harrison Lakes. ONEIDA CO: Bearskin, Dorothy, Little Bearskin, North Two, Sand, Spirit, Squash, Virgin, and Whitefish Lakes. VILAS CO: Crab, Deadman, and Rice Lakes; and Lac Vieux Desert.

13. **N. linearis** (C.A. Ag.) W. Smith, 1853. (Figures 32–33).

DESCRIPTION: Valves linear, 103–263 μm long and 4.5–6.5 μm wide, with a distinct central constriction along one margin; apices capitate; striae finely punctate, parallel, 28 30 per 10 μm; keel marginal, usually with a distinct central nodule; fibulae 7 11.1 per 10 μm.

FOREST CO: Himley and Silver Lakes. IRON CO: Clear, Lower Springstead, Mercer, and Trude Lakes; and Lake-of-the-Falls. LINCOLN CO: Pine Lake, ONEIDA CO: Horsehead, Minocqua, Nokomis, Pelican, Rainbow, Spirit, Squash, and Whitefish Lakes. PRICE CO: Pike Lake. VILAS CO: Big, Big Gibson, Big Sand, Black Oak, Crab, Diamond, Palmer, Presque Isle, and Star Lakes; and Lac Vieux Desert.

14. **N. palea** (Kütz.) W. Smith var. **palea,** 1856. (Figures 12–14).

DESCRIPTION: Valves linear to linear-lanceolate, 22 42 μm long and 3 5 μm wide; apices rostrate or mildly capitate; striae finely punctate, scarcely visible under LM; keel marginal, usually without a conspicuous central nodule; fibulae 10.7–15.1 per 10 μm.

FOREST CO: Bug and Wabikon Lakes. IRON CO: Trude Lake; and Lake-of-the-Falls. LINCOLN CO: Clara, Harrison, and Pine Lakes. ONEIDA CO: Bearskin, Crescent, Katherine, North Two, Rainbow, Sand, Spirit, Squash, and Whitefish Lakes. PRICE CO: Butternut, Cranberry, Duroy, Elk, Long, and Solberg Lakes. VILAS CO: Big Arbor Vitae, Big Muskellunge, Big Sand, Crab, Eagle, Flambeau, Nichols, and North Twin Lakes; and Lac-du-Lune and Lac Vieux Desert.

15. **N. palea** var. **tenuirostris** Grunow *sensu* Hustedt *In:* Pascher, 1930. (Figure 15).

DESCRIPTION: Valves narrowly linear to linear-lanceolate, 33–70 μm long and 3–4.5 μm wide; apices protracted, slightly capitate; striae finely punctate, scarcely visible under LM; keel marginal, usually without a conspicuous central nodule; fibulae 12 17.6 per 10 μm.

FOREST CO: Deep Hole and Ground Hemlock Lakes. IRON CO: Mirror Lake; and Lake-of-the-Falls. LINCOLN CO: Clara and Pine Lakes. ONEIDA CO: Horsehead, Katherine, Little Bearskin, Squash, and Washburn Lakes. PRICE CO: Pike Lake. VILAS CO: Big Muskellunge, Big Sand, Black Oak, Crab, Eagle, Ike Walton, Rice, and Spider Lakes; and Lac-du-Lune.

16. **N. recta** Hantz. *In:* Cleve and Grunow, 1880. (Figure 22).

DESCRIPTION: Valves linear, 69 97 μm long and 5.5–8 μm wide; apices generally tapered, acutely rounded; striae finely punctate, scarcely visible under LM; keel marginal, without a conspicuous central nodule; fibulae robust, about 6–7 per 10 μm.

FOREST CO: Rice and Silver Lakes. ONEIDA CO: Crescent Lake. VILAS CO: Duroy Lake.

17. **N. romana** Grun. *In:* Van Heurck, 1881. (Figures 6–7).

DESCRIPTION: Valves narrowly lanceolate, 23–56 μm long and 2–3.5 μm wide; apices acutely rounded; striae indistinctly punctate, parallel, 24–30 per 10 μm; keel marginal, usually without a conspicuous nodule; fibulae 9.3–12.6 per 10 μm.

FOREST CO: Richardson Lake. IRON CO: Clear Lake; and Lake-of-the-Falls. ONEIDA CO: Bearskin, Crescent, Horsehead, Katherine, Little Bearskin, Little Tomahawk, Nokomis, Pelican, Spirit, Squash, Virgin, and Whitefish Lakes. PRICE CO: Butternut and Pike Lakes. VILAS CO: Big Muskellunge, Big Sand, Black Oak, Catfish, Eagle, Flambeau, and Star Lakes; and Lac Vieux Desert.

18. **N. sigmoidea** (Nitz.) W. Smith, 1853. (Figure 31).

DESCRIPTION: Valves linear, 173–450 μm long and 8–14 μm wide; apices acutely rounded, cuneate and slightly recurved; striae indistinctly punctate, parallel, ca. 23 24 per 10 μm; keel marginal, generally without a conspicuous central nodule; fibulae robust, about 5–7 per 10 μm.

COMMENTS: This taxon is easily recognizable from most other species of *Nitzschia* in that it is distinctly sigmoid in outline when seen in girdle view.

FOREST CO: Himley, Mole, and Wabikon Lakes. IRON CO: Trude Lake; and Lake-of-the-Falls. ONEIDA CO: Bearskin and Whitefish Lakes. VILAS CO: Big Arbor Vitae Lake.

19. **N. sinuata** var. **delongei** Lange-Bertalot, 1980. (Figure 29).

DESCRIPTION: Valves lanceolate, 10–27 μm long and 3–3.5 μm wide; apices subcapitate; striae punctate, parallel, 23–26 per 10 μm; keel marginal, usually without a conspicuous central nodule; fibulae robust and costa-like, usually extending about half-way into the center of the valve, 4.5–5.6 per 10 μm.

IRON CO: Mercer Lake. ONEIDA CO: Bearskin Lake. VILAS CO: Crab Lake.

20. **N. sinuata** var. **tabellaria** (Grun.) Grun. *In:* Van Heurck, 1885. (Figure 30).

DESCRIPTION: Valves lanceolate, 17–21 μm long and 7–7.5 μm wide, with broadly inflated central margins; apices capitate; striae punctate, parallel, about 18 per 10 μm; keel marginal, usually without a conspicuous central nodule; fibulae robust and costa-like, usually extending about half-way into the center of the valve, ca. 5.2 per 10 μm.

ONEIDA CO: Nokomis Lake.

21. **N. tryblionella** Hantz. *In:* Cleve and Grunow, 1880. (Figure 27).

DESCRIPTION: Valves elliptic-lanceolate, about 66 μm long and 21 μm wide, usually with distinct longitudinal folds; apices rounded, slightly cuneate; striae robust, parallel at the center of the valve, becoming slightly convergent toward the apices, usually 7–9 per 10 μm; keel marginal, usually with a distinct central nodule; fibulae large, about 5.8 per 10 μm.

PRICE CO: Duroy Lake.

22. **N. valdestriata** Aleem and Hustedt, 1951. (Figure 28).

DESCRIPTION: Valves linear, 8–13 μm long and 2.5 μm wide; apices rounded; striae indistinctly punctate, usually parallel at the center of the valve, becoming slightly radiate toward the apices, 12.5–15 per 10 μm; keel marginal, usually with a distinct central nodule; fibulae 7.5–8.8 per 10 μm.

ONEIDA CO: Katherine and Squash Lakes. VILAS CO: Big Arbor Vitae, Crab, Flambeau, and Spider Lakes.

DISCUSSION

Four taxa previously reported from the Highland Lake District, but not recorded during this investigation, are *Nitzschia acuta* Hantz. *ex* Grun., *N. gracilis* Hantz., *N. sublinearis* Hust., and *N. vermicularis* (Kütz.) Grun. (Conger, 1939; Lipsey and Fenwick,

1978). Twelve taxa are new Wisconsin records: *Hantzschia amphioxys* var. *vivax, H. elongata, Nitzschia angustata, N. angustata* var. *acuta, N. denticula, N. dissipata* f. *undulata, N. hollerupensis, N. intermedia, N. palea* var. *tenuirostris, N. sinuata* var. *delognei, N. sinuata* var. *tabellaria,* and *N. valdestriata.*

The species and subspecific taxa described in this paper generally occur in the littoral regions of lakes within the district and may at times form an important component of the benthic flora. When abundant *Nitzschia denticula, N. dissipata,* and *N. linearis* are indicative of oxygen-rich waters (Schoeman, 1976). However, as a rule, *Nitzschia* is most often associated with nutrient-rich waters (Hustedt, 1957). For example, *N. acicularis, N. amphibia, N. fonticola, N. gandersheimiensis, N. intermedia, N. palea,* and *N. sigmoidea* are mostly reliable indicators of organic pollution or nitrogen enriched waters (Lange-Bertalot, 1979; Lowe, 1974; Palmer, 1963; 1969; Schoeman, 1976). Therefore, the presence or absence of these species in lakes may provide a means of assessing water quality.

Nitzschia acuta, N. amphibia, N. gracilis, N. palea, and *N. sigmoidea* have been reported in southeastern Wisconsin by Sloey and Blum (1972). Occurrences of *Hantzschia amphioxys, Nitzschia amphibia, N. linearis,* and *N. palea* in southwestern Wisconsin are included in the reports of Andrews (1966) and Strenski (1979). *Hantzschia amphioxys* var. *capitata* Pant., *Nitzschia filiformis* (W. Sm.) Hust., *N. spectabilis* (Ehrenb.) Ralfs, and *N. thermalis* (Ehrenb.) Grun. have also been recorded from the inland waters of southern Wisconsin (Andrews, 1966; Sloey and Blum, 1972), and Vansteenburg et al. (1984) have reported 16 additional taxa (including the genus *Bacillaria* Gmelin) from the Mississippi River along the southwestern Wisconsin border.

ACKNOWLEDGMENTS

I thank Mark Mohlenbrock for preparing the line drawings used to illustrate this paper.

LITERATURE CITED

ALEEM, A., AND F. HUSTEDT. 1951. Einige neue diatomeen von der Sudkuste Englands. Bot. Not. 1951: 13 20.

ANDREWS, G. W. 1966. Late Pleistocene diatoms from the Trempealeau Valley, Wisconsin. U.S. Geol. Surv. Prof. Pap. 523: 324-333.

CLEVE, P. T., AND A. GRUNOW. 1880. Beiträge zür kenntis der arctischen Diatomeen. K. Svenska Vetensk.-Akad. Handl. 17: 1–121.

CONGER, P. S. 1939. The contribution of diatoms to the sediments of Crystal Lake, Vilas County, Wisconsin. Amer. J. Sci. 237: 324–340.

FOGED, N. 1962. On the diatom flora in interglacial Kieselguhr at Hollerup in East-Jutland. Bull. Geol. Surv. Denmark 2: 1–51.

GRUNOW, A. 1862. Die österreichischen Diatomeen nebst Anschluss einiger neuer Arten von anderen lokalitäten und einer kritischen ubersicht der bisher bekannten Gattungen und Arten. Zweite folge. Family Nitzschieae. Verh. Zool.-Bot. Ges. Wien 12: 545 585.

HUSTEDT, F. 1930. Bacillariophyta. *In:* A. Pascher, "Die Susswasser-Flora Mitteleuropas". Heft 10, Jena, G. Fischer.

———. 1954. Die diatomeenflora des interglazials von Oberohe in der Lüneburger Heide. Abh. Naturwiss. Verein Bremen 33: 453.

———. 1957. Die diatomeenflora des Flusssystems der Weser im Gebiet der Hansestadt Bremen. Abh. Naturwiss. Verein Bremen 34: 181–440.

KARSTON, G. 1928. Bacillariophyta (Diatomeae). *In:* Engler & Prantl, "Die natürlichen Pflanzenfamilien", 2: 105–303.

KRASSKE, G. 1927. Diatomeen deutscher Solquellen unde Gradierwerke I. Arch. Hydrobiol. 18: 252 272.

LANGE-BERTALOT, H. 1977. Eine revision zur taxonomie der Nitzschiae lanceolatae Grunow. Die "klassischen" bis 1930 beschriebenen Süsswasserarten Europas. Nova Hedwigia 28: 253–307.

———. 1979. Pollution tolerance of diatoms as a criterion for water quality estimation. Nova Hedwigia Beih. 64: 285–304.

———. 1980. New species, combinations and synonyms in the genus *Nitzschia*. Bacillaria 3: 41–77.

———, AND R. SIMONSEN. 1978. A taxonomic revision of the Nitzschiae lanceolatae Grunow. 2. European and related extra-European freshwater and brackish water taxa. Bacillaria 1: 11–111.

LIPSEY, L. L. 1987. Freshwater diatoms (Bacillariophyceae) from the northeastern glacial lake district of Wisconsin. I. *Attheya, Cyclotella, Melosira, Rhizosolenia,* and *Stephanodiscus* (Order Centrales). Rhodora 89: 261–278.

———, AND M. G. FENWICK. 1978. Investigations on the freshwater algae of Wisconsin. I. Plankton diatoms from High Lake (Vilas County). Michigan Bot. 17: 113–117.

LOWE, R. L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. U.S. E.P.A., Report #670/4–74–005, Environmental Monitoring Series, Cincinnati, Ohio.

MANN, D. G. 1977. The diatom genus *Hantzschia* Grunow - an appraisal. Nova Hedwigia Beih. 54: 323–354.

———. 1980. *Hantzschia fenestrata* Hust. (Bacillariophyta) — *Hantzschia* or *Nitzschia?* Brit. Phycol. J. 15: 249–260.

PALMER, C. M. 1963. The effect of pollution on river algae. Ann. New York Acad. Sci. 108: 389–395.

———. 1969. A composite rating of algae tolerating organic pollution. J. Phycol. 5: 78–82.

REIMER, C. W. 1953–54. Re-evaluation of the diatom species *Nitzschia frustulum* (Kütz.) Grun. Butler Univ. Bot. Stud. 11: 178–191.

SCHMIDT, A. 1874–1959. Atlas der Diatomaceen-Kunde. Continued by M. Schmidt, F. Fricke, H. Heiden, O. Müller, and F. Hustedt. R. Reisland, Leipzig.
SCHOEMAN, F. R. 1970. Diatoms from the Orange Free State (South Africa) and Lesotho. No. 3. Bot. Mar. 13: 49 72.
_____. 1976. Diatom indicator groups in the assessment of water quality in the Jukskei-Crocodile River system (Transvaal, Republic of South Africa). J. Limnol. Soc. S. Africa 2: 21–24.
_____, AND R. E. M. ARCHIBALD. 1976. The Diatom Flora of Southern Africa. Explanatory Notes (1). No. 1, September 1976. CSIR Special Report WAT 50.
_____, AND P. J. ASHTON. 1982. The diatom flora in the vicinity of the Pretoria Salt Pan, Transvaal, Republic of South Africa I. Nova Hedwigia Beih. 73: 21–54.
_____, R. E. M. ARCHIBALD, AND _____. 1984. The diatom flora in the vicinity of the Pretoria Salt Pan, Transvaal, Republic of South Africa. Part III (final). S. African J. Bot. 3: 191–207.
SCHÜTT, F. 1896. Bacillariales (Diatomeae). *In:* Engler & Prantl, "Die naturlichen Pflanzenfamilien", 1: 31–150.
SIMONSEN, R. 1979. The diatom system: Ideas on phylogeny. Bacillaria 2: 9 71.
SLOEY, W. E., AND J. L. BLUM. 1972. The algae of the Winnebago Pool and some tributary waters. Trans. Wisconsin Acad. Sci., Arts & Let. 60: 125–145.
SMITH, W. 1853–1856. A Synopsis of the British Diatomaceae; with Remarks on Their Structure, Functions and Distribution; and Instructions for Collecting and Preserving Specimens. London, John van Voorst. Vol. 1., Vol. 2.
SOVEREIGN, H. E. 1963. New and rare diatoms from Oregon and Washington. Proc. California Acad. Sci. 31: 349 368.
STRENSKI, M. R. 1979. The phycoperiphyton community of the Lower Black River, Wisconsin. Trans. Wisconsin Acad. Sci., Arts & Let. 67: 69 77.
TYNNI, R. 1980. Über Finnlands rezente und subfossile Diatomeen, XI. Bull. Geol. Surv. Finland 312: 1–93.
VAN HEURCK, H. F. 1880–1885. Synopsis des Diatomées de Belgiqúe, Atlas et texte. Anvers.
VANSTEENBURG, J. B., M. R. LUTTENTON, AND R. G. RADA. 1984. A floristic analysis of the attached diatoms in selected areas of the upper Mississippi River. Proc. Iowa Acad. Sci. 91: 52–56.

ILLINOIS ENVIRONMENTAL PROTECTION AGENCY
CHICAGO LABS / WATER MICROBIOLOGY UNIT
2121 W. TAYLOR
CHICAGO, IL 60612

RHODORA, Vol. 90, No. 864, 1988

BUFFALO CLOVERS IN KENTUCKY (*TRIFOLIUM STOLONIFERUM* AND *T. REFLEXUM*): HISTORICAL RECORDS, PRESETTLEMENT ENVIRONMENT, REDISCOVERY, ENDANGERED STATUS, CULTIVATION AND CHROMOSOME NUMBER

JULIAN J. N. CAMPBELL, MARC EVANS, MAX E. MEDLEY AND NORMAN L. TAYLOR

ABSTRACT

Currently, Kentucky's two native *Trifolium* species, *T. stoloniferum* and *T. reflexum*, are each known from only one locality. Historical records indicate that *T. stoloniferum* was widespread on moist, fertile soils in the Bluegrass Region, and that *T. reflexum* occurred on drier or less fertile soils in the fomer Big Barrens Region and the Shawnee Hills. Many old records are from areas with open woodland or grassland disturbed by Indians and buffalo (*Bison*), and recent records are mostly from roadsides or trails through woods. The decline of these species may be attributed to changes in disturbance and consumer patterns since settlement. In cultivation, *T. stoloniferum* is a vigorous perennial, easily propagated from stolons, but it requires moist, fertile soil, and is sensitive to competition and herbivory. *Trifolium reflexum* grows more slowly and is typically biennial. The chromosome number of *T. stoloniferum*, reported here for the first time, is the same as other eastern North American species ($2n = 16$).

Key Words: *Trifolium stoloniferum*, *Trifolium reflexum*, buffalo clover, endangered species, chromosome number, Bluegrass Region, Big Barrens Region, Kentucky

INTRODUCTION

Two native species of clover (*Trifolium*) are known in Kentucky; both are extremely rare. In this paper, we combine historical and modern records of these species from the state for an initial examination of their unusual ecology. To determine all known records and references, we have searched herbaria in Kentucky and elsewhere, and we have searched the botanical and historical literature. The early common name for these species—"buffalo clover" suggests that they were associated with buffalo (*Bison*) in the presettlement landscape; this conjecture is supported by our historical data. We have also begun to cultivate both species, and have some preliminary observations on their growth. Eventually, we hope to understand why they have become so rare since settlement, and how we can reintroduce and maintain them in protected areas.

This paper is concerned primarily with two areas of Kentucky. The Bluegrass Region is mostly on Ordovician limestones and calcareous shales. Some Inner Bluegrass soils are particularly fertile, with high prosphate levels, but Eden Shale soils tend to have lower fertility (U.S.D.A. Soil Conservation Service, 1975). Before settlement, richer soils were largely forested with *Acer saccharum* Marsh., *Juglans nigra* L., *Quercus* spp., *Fraxinus* spp. and *Carya* spp. Some relatively open areas were covered by *Arundinaria gigantea* (Walt.) Chapman ("cane") and other grasses (Bryant *et al.*, 1980; J. Campbell, 1980, Ph.D. diss., Univ. of Kentucky). On poorer soils, the vegetation was mostly *Quercus-Carya* and *Fagus* forest. The other area is the former Big Barrens Region (Pennyrhile section of the Mississippian Plateaus), which is mostly calcareous, and the adjacent Shawnee Hills Region (Western Coal Field of Pennsylvanian age), which is non-calcareous. Upland soils in this area generally have lower fertility than the Bluegrass, and the limestone sections are generally drier. The predominant upland vegetation before settlement was *Quercus-Carya* forest or, on much of the limestone, grassland (Braun, 1950; Baskin and Baskin, 1981).

The two clover species have often been confused. They differ in the following characters (modified from Brooks, 1983):

Trifolium stoloniferum Muhl. ex Eaton: perennial, without rosette, stoloniferous; plant glabrous or sparsely puberulent; leaflets nearly as wide as long, unmarked; flowering in mid-April to June, the stems unbranched, with two leaves and one head (rarely two) at apex; corolla white or tinged with pink-purple veins; seeds 1.7 -2.0 mm long, smooth.

Trifolium reflexum L.: biennial or winter annual, forming an overwintering rosette, non-stoloniferous; plant densely pubescent or (to the north) glabrate; leaflets much longer than wide, often marked with purplish bands; flowering in mid-May to July, the stems often branched, leafy, with one to several heads from upper axils; corolla, at least the standard, generally red or pink, rarely (to the west) all white; seeds 1.2 1.5 mm long, obscurely verruculose or ridged.

TRIFOLIUM STOLONIFERUM MUHLENBERG *EX* A. EATON 1818

Brooks (1983) mapped the historical records of *Trifolium stoloniferum*, which are from several east-central states (Figure 1); he found no reports later than 1940. It was rediscovered in West Virgi-

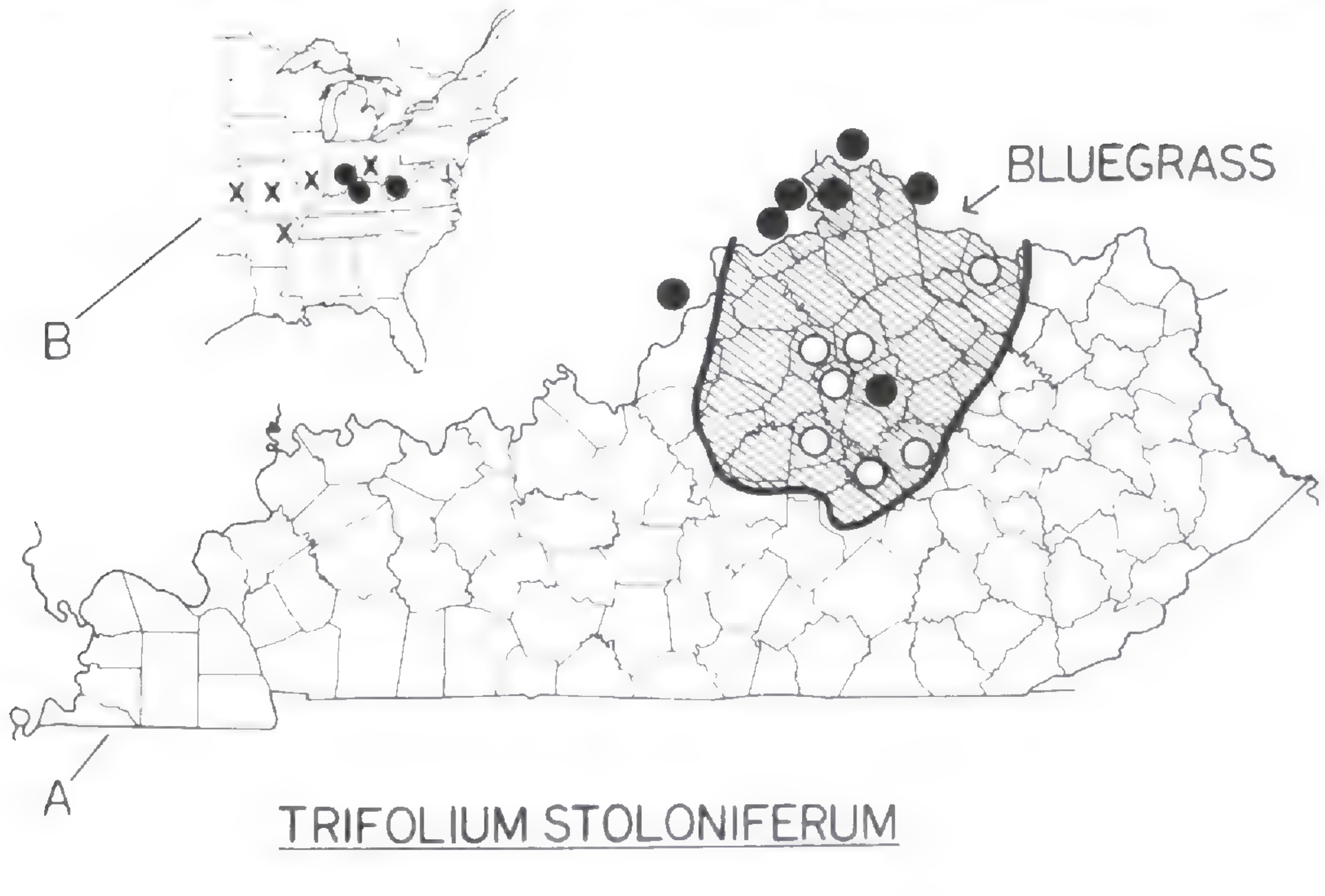


Figure 1. Distribution of *Trifolium stoloniferum* in Kentucky and the Eastern United States.
A. Kentucky. Solid dots show counties with collections known; open dots show counties with unvouched reports or historical indications of the species. The Bluegrass Region (on Ordovician bedrock) is shaded.
B. Eastern U.S. Solid dots show states with wild plants still known; X's show states with old collections but no sites currently known to active botanists (mostly from Brooks, 1983).

nia during 1983–84 (Bartgis, 1985), and in southeastern Indiana (M. Homoya and J. Aldrich, Indiana Natural Heritage Program, pers. comm.) and northern Kentucky (see below) during 1987. The U.S. Fish and Wildlife Service (1987) has listed it as "endangered".

Collection Data (herbarium acronyms from Holmgren et al., 1981).

1. C. W. Short: 1835 (GH); April–May (PH, KY); May (F, NY); no data (CLM, KY, PH). Some labels are printed with "Lexington", where Short (and his colleague R. Peter) resided and collected during 1825–45.

2. R. Peter: May 1834, fields about Lexington (MICH, NY); June 1835, meadows etc. about Lexington, Fayette Co., 'Buffalo Clover' (PH)

3. W. A. Kellerman, May 10, 1882, no further data (KANU, KSC).

4. H. Garman, May 11, 1902, Mt. Tabor Pike, Lexington (KY)—Dept. of Agronomy). Misidentified as *Trifolium reflexum*.

5. M. Evans, June 25, 1987, Boone County, northeast of Belleview on lower wooded slopes bordering Ohio River bottomland (EKU). The exact location is with the Kentucky Nature Preserves Commission. *Trifolium stoloniferum* grows in two patches, one with about 50 plants covering a 3 m × 5 m area along a path, the other with several hundred plants covering a 5 m × 15 m area in a nearby clearing adjacent to an old cemetery. The plants grow in rich loam under a tree canopy closure of 50 80%. According to the landowner, the site was an open pasture until 40–50 years ago; both patches are mowed annually. Woody associates include *Carya cordiformis* (Wang) K. Koch, *Liriodendron tulipifera* L., *Fraxinus americana* L., *Acer negundo* L., *Quercus alba* L., *Prunus serotina* Ehrh., *Cercis canadensis* L., *Lindera benzoin* (L.) Blume and *Sassafras albidum* (Nutt.) Nees. Herbaceous associates include *Impatiens pallida* Nutt., *Pilea pumila* (L.) Gray, *Leersia virginia* Willd., *Juncus tenuis* Willd., *Eupatorium rugosum* Houtt., *Cryptotaenia canadensis* (L.) DC., *Elymus* spp. and *Alliaria officinalis* Andrz. (an exotic dominant in the woods).

Other Possible Records. Evidence that the following records refer, in general, to *Trifolium stoloniferum* is detailed in the Discussion section, with notes on common names. All records are from the Bluegrass Region, ranging from descriptions of the pioneers, who first arrived in the 1770's, to later academic notes. They are a major source of information on the environment during early settlement.

6. James McAfee (1773, in Woods, 1905, p. 435) travelled from near the Dix River towards the east (Garrard County) on August 1: "We left Rock Camp, travelled mostly an eastern course about 16 miles amongst broken ridges covered with cane and clover. . ."

7. Hanson (1774, in Thwaites and Kellogg, 1905, p. 130) surveyed "on the North Branches of Elkhorn Creek, about seven or eight miles from the fork" (Scott County) on July 8: "The land is so good that I cannot give it due praise. Its undergrowth is clover, pea-vine, cane & nettles - intermixed with rich weed. Its timber is honey locust, black walnut, sugar tree, hickory, iron-wood, hoop-wood [=*Celtis*?], mulberry, ash and elm and some oak." This area was on or within a mile of the large buffalo road that ran from Sand Lick to Stamping Ground (Jillson, 1934; J. Sames, pers. comm.).

8. Henderson (1775, in Ranck, 1901, p. 170) described the large elm tree on the Kentucky River bottom at Boonesborough (Madison County) on May 14: "This tree is placed in a beautiful plain surrounded by a turf of white clover forming a green to its very stock. . ." Ranck (1901, p. 18) described the lick here in 1775: "The

rich soil, thanks to generations of animals that had haunted the lick, was open, firm, and almost free from undergrowth, and, except about the trampled lick and in the broad buffalo path, was adorned, early as it was, with great patches of fine white clover and thickly carpeted with a natural grass. . . Kentucky bluegrass."

9. Cresswell (1775, printed in 1925, p. 76) described the Ohio Valley opposite the mouth of the Great Miami River (Boone County) on May 19: "It is a little hilly but rich beyond conception. Wild clover, what they here call Wild Oats and Wild Rye in such plenty it might be mown and would turn out a good crop. The great quantity of grass makes it disagreeable walking . The land is thin of timber and little underwood." He also noted Indians and buffalo in the area.

10. Nourse (1775, printed in 1925, p. 252) described land southeast of Frankfort (Franklin to Woodford County) on May 30: "It is about 2 miles from the river on top of the Hill, the land is level and well timbered with oak, afterwards it is light with timber—little oak—mostly sugar tree, Walnut, Ash and Buckeye (horse chestnut) but the tops of the trees mostly scraggy, the surface of the ground covered with grass along the path which was as well trod as a Market-town path. About Twelve mile, the farther we went the richer the land, better though of the same sort of timber, the ash very large and high, and large locusts of both sorts—some cherry – the growth of the grass under amazing—blue grass, white clover, buffalo grass and seed knee and waist high: what would be called a fine swarth of Grass in cultivated Meadows, and such was its appearance without end - in little dells in this. We passed several dry branches but no running water our course S.E. At about twelve mile came to a Small run. . . We had seen in our walk about 5 herd of Buffaloes." His route was probably along the large buffalo road that is closely followed by State Route 1681 or "Old Frankfort Pike" (Jim Sames, pers. comm.).

11. Filson (1784, p. 9 -13) described "The Elkhorn Lands" (Inner Bluegrass): "This great tract is beautifully situated, covered with cane, wild rye, and clover. . . Where no cane grows, there is an abundance of wild-rye, clover and buffalo-grass, covering vast tracts of country, and affording excellent food for cattle."

12. Morse (1789, p. 404) also described the Inner Bluegrass in general: "The soil is deep and black, and the natural growth, large walnuts, honey and black locust, poplar, elm, oak, hickory, sugar tree, etc. Grape vines running to the tops of the trees, and the surface covered with clover, blue grass and wild rye."

13. Anonymous (1791, in Schwaab, 1973, p. 55) described the route from Maysville (Mason County) to Lexington: "You frequently find beds of clover to the horse's knees, sometimes a species of rush-grass commonly called wild rye. . ." This road had been one of the major buffalo trails in the region (Jillson, 1934).

14. Imlay (1792, p. 29–32) also described the road from Maysville (Mason County): "From Limestone to Johnson's Fork of Licking Creek, the country is immensely rich, and covered with cane, rye-grass, and the native clover. . . in no respect different from the clover in Europe, but as it is more coarse and luxuriant."

15. Harris (1797, printed in 1928, p. 166) described land in and around Mason County: "To innumerate all the natural herbage & flowers in the woods would be too tedious & I should want names for them; Buffaloe Clover, Rye grass —pea vine & a broad leaf grass & what is call'd rich weed is what the Cattle most delight in."

16. Marshall (1812, p. 5) described pioneers in the Inner Bluegrass about 1779: "Their arrival on the plains of Elkhorn, was in the dawn of summer, when the forest composed of oaks of various kinds, of ash, of walnut, cherry, buckeye, hackberry, sugar trees, locust, sycamore, coffee tree, and an indefinite number of other trees, towering aloft to the clouds, overspread the luxuriant undergrowth, with their daily shade, while beneath, the class of trees — the shrubs, the cane, the herbage, and the different kinds of grass, and clover, interspersed with flowers, filled the eye, and overlaid the soil with the forest's richest carpet."

17. Felix Walker (1824, in Ranck, 1901, p. 162) recalled the "plains of Kentucky," in and around Madison County, when he arrived in late March, 1775: "So rich a soil we had never seen before; covered with clover in full bloom. . ."

18. John Bradford (1827, in Townsend, 1932, p. 119) related the speech of Simon Girty in 1782, urging Indians to attack Bryan's Station (Fayette County): "Brothers: the fertile region of Kentucky is the land of cane and clover — spontaneously growing to feed the buffaloes, the elk and the deer. . . Brothers: the long knives. . . have destroyed the cane — trodden down the clover. . . They are planting fruit trees and ploughing the land where not long since were the cane break and clover field." According to Samuel Matthew (L. Draper's Manuscripts, 1840s, Wisc. Hist. Soc., 11CC: 158), the Bryan's Station area in 1783 was covered with woods containing dense cane or: "Land that had not cane on it, was grown up with white blossoms, and the trees were tall ash, sugar-trees, elms, hackberry, tall and very thick." Bryan's Station was located on the large buffalo road from Lexington to Blue Licks to Maysville (Jillson, 1934).

19. Levi Todd (L. Draper's Manuscripts, 1840s, Wisc. Hist. Soc., 15CC: 157–162) described the land around Lexington (Fayette County) in 1776: "nearly one-half of it covered with cane, but between the brakes, spaces of open ground as if intended by nature for fields. The ground appeared fertile, and producing amazing quantities of various kinds, some wild grass, wild rye and clover."

20. Robert Gwynne (L. Draper's Manuscripts, 1840s, Wisc. Hist. Soc., 11CC: 217) described Woodford County in or after 1784: "The Shawnee Run Indian trace was never more than a foot wide, was a foot deep. It passed thro' Clover bottom, where Mr Clanahan made a pre-emption, called so bec[au]s[e] the Buffalo clover grew up there in a little space, about twice as big as this house (a stone house w[ith] 3 rooms on the ground floor)." Clover Bottom remains a place name today.

21. Robert McAfee (1845, printed in 1927 p. 113) described what cattle eat when the Inner Bluegrass (especially Mercer County) was first settled: "The cane, peavine and wild grass and clover called buffalo clover (a large white kind) supplied them with pasturage with little feeding (except salting) both winter and summer."

22. Draper (1851, in Hanna, 1911, p. 232) described pioneer times in central Kentucky, according to Nathan Boone: "Buffaloes were in the best order in the fall, after feeding upon wild grass, buffalo clover, and pea-vine, and to some extent also, upon acorns, beech-nuts and chestnut; the clover, a kind with a large white blossom, lasting the whole growing season, but the pea vine only affording sustenance in the latter part of summer and early autumn."

23. Perrin (1882) stated in his Fayette County History: "we now sometimes see a specimen of 'buffalo clover'. This has a large white blossom, is intermediate between the common white and red clover, and is only to be found in very shaded places. It will not grow in open ground, and is of little value for animals food..." But note J. G. Smith (1896) on *T. stoloniferum*: "greedily eaten by cattle. It should be given a trial in cultivation."

24. Wm. Chenault (ca. 1884, in Dorris, 1932, p. 120) described the settlement of Madison County: "The white men who first came within its borders in 1770, 1773 & 1774, found that its trees consisted of the maple, ash, elm, black walnut, oak, mulberry, sycamore and cedar, with many groves of honey locust scattered along the bank of Silver Creek. The undergrowth was clover, pea-vine, cane, nettle, rye and blue or English grass as it was more generally called by the early settlers."

25. Nelson (1919) listed plants collected in Boone County during 1881–93, with no herbarium noted: "*Trifolium soloniferum*

Muhl. Occasional in open ground." He also listed *T. pratense* and *T. repens*.

26. Edna Kenton (1930, p. 6) described the Bluegrass Region when her ancestor, Simon Kenton, arrived in the 1770s: "It was carpeted with wild rye, with prairie and buffalo clover, with the deep "blue grass" and with "Rich Weed"..."

TRIFOLIUM REFLEXUM LINNAEUS 1753: 766

Trifolium reflexum used to occur in most states east of the Great Plains and south of the Great Lakes (Figure 2). It may still be relatively widespread in Missouri (Steyermark, 1963) and perhaps Arkansas. However, there are post-1950 records from only one to three counties each in Nebraska, Iowa, Illinois, Indiana, Kentucky and Tennessee, and the species has disappeared from Ohio, West Virginia, Virginia, Pennsylvania, Maryland, New York and Onta-

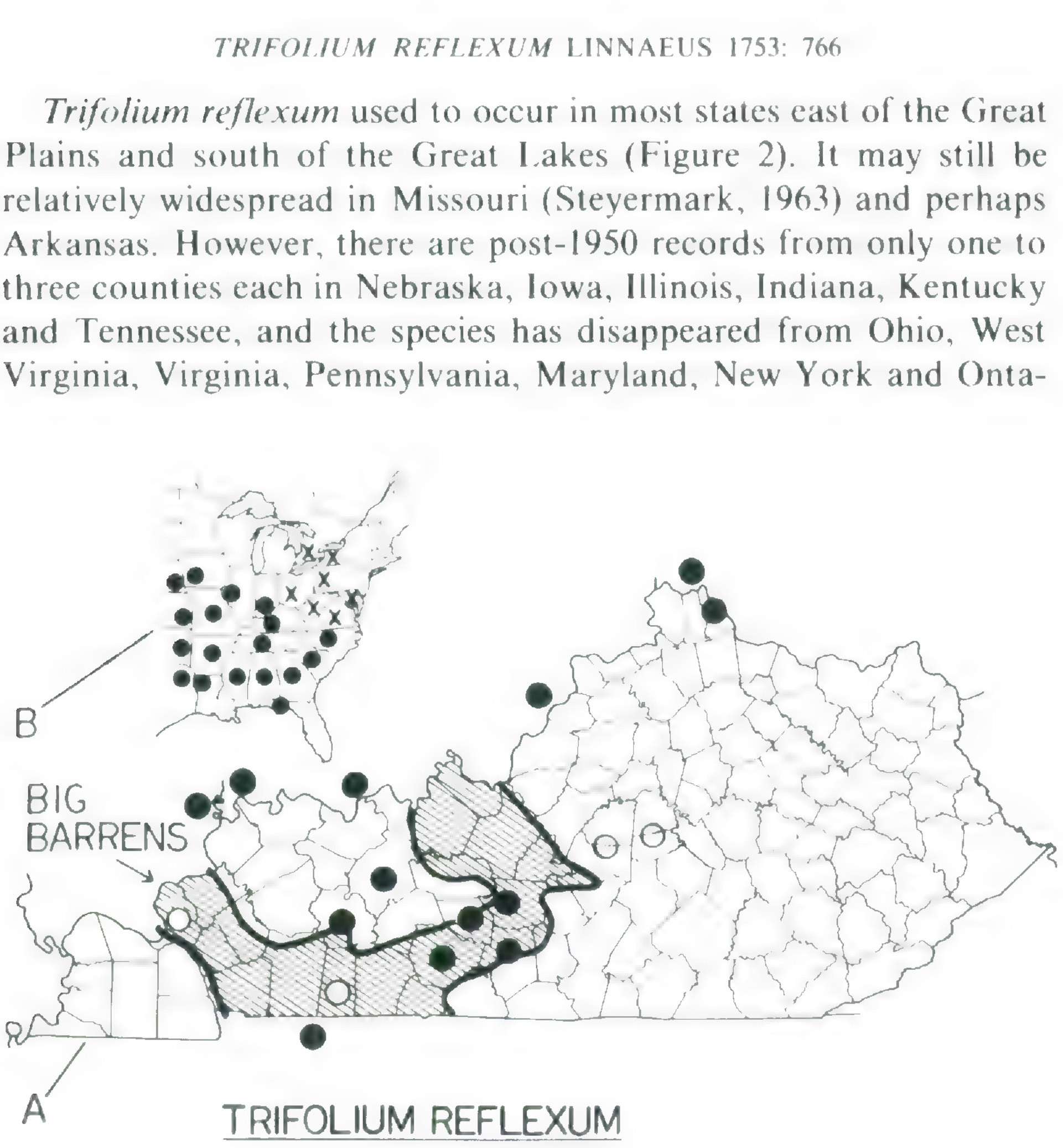


Figure 2. Distribution of *Trifolium reflexum* in Kentucky and the Eastern United States. Symbols are the same as in Figure 1.

A. Kentucky. The former Big Barrens Region (on Upper Mississippian bedrock) is shaded; between this region and the Ohio River are the Shawnee Hills, on Pennsylvanian bedrock.

B. Eastern U.S. Data are taken from existing State Floras and Atlases, and from personal communication with several authorities in various states (see Acknowledgments).

rio. Northern populations are mostly var. *glabrum* Lojacono, but this taxon may only represent one extreme of a cline (Isely, 1951, and pers. comm.).

Collection Data.

1. C. W. Short, June [ca. 1825 45], fields and roadsides among the barrens (PH).

2. C. W. Short, [ca. 1825 454], Licking River (PH). Perhaps near (3).

3. T. G. Lea, No. 620258 [1834 44], beach, Dayton [Campbell Co.] (PH).

4. J. Hussey, Kriebel Herbarium Nos. 11881/2/3/5, May 23-26, 1874: near Glasgow [Barren County], yellow; near Mammoth Cave [Edmonson County]; Barren County; Edmonson County (all at PUL).

5. J. H. Barnhart, No. 2291, May 30, 1897, open woods, Mammoth Cave [Edmonson County] (NY).

6. C. G. Lloyd, 1897, Mammoth Cave (GH).

7. Sadie N. Price, [ca. 1885 1910], Bowling Green [Warren Co.] (NY).

8. J. W. Barkley, June 8, 1897, Greenville, Muhlenberg Co. (KY - Dept. of Agronony). H. Garman (1902) apparently grew seed from this collection, leaving a specimen from cultivation: 11 June 1898, grown from seed, Vivarium, Lexington (KY - Agron.).

9. R. Holbrook, June 3, 1907, Hartford [Ohio County] (KY - Agron.).

10. Anon. [perhaps H. Garman], May 19, 1910, Lex., Ky (KY - Agron.).

11. J. C. Morton, May 20, 1915, Centertown [Ohio Co.] (KY - Agron.).

12. C. Weatherby, May 22, 1933, Mammoth Cave (GH).

13. N. L. Taylor and T. H. Taylor, June 1976, Mammoth Cave National Park, Edmonson County (KY - Agron.). We have stored seed from this collection. About 100–200 plants occurred along a road through young mixed forest on gently sloping limestone uplands. In 1987 we could only find two flowering plants and about 20 seedlings. Associated species in 1987 included *Quercus alba* L., *Cornus florida* L., *Amphicarpaea bracteata* (L.) Fern., *Anemone virginiana* L., *Krigia biflora* (Walt.) Blake, *Erigeron pulchellus* Michx., *Parthenocissus quinquefolia* (L.) Planch., *Antennaria plantaginifolia* (L.) Richards and *Muhlenbergia sobolifera* (Muhl.) Trin.

H. Holman, Park Naturalist, (pers. comm.) has found two other populations in the Park.

14. N. L. Taylor, 1977, along a dirt road between woods and fields near Mammoth Cave National Park, Hart County (KY - Agron.). Seed only was collected. Fewer than 10 plants were seen.

Some of these collections (at least 8–11, previously misidentified as *Trifolium stoloniferum*) conform to var. *glabrum*, with virtually no pubescence and up to 30–40 cm tall—others are mostly 20–30 cm tall. Collections misidentified as *T. reflexum* include H. Garman's *T. stoloniferum* from Lexington (see above) and E. M. & E. T. Browne's *T. pratense* L. from Bourbon County (E. Guhardja, 1962, M.Sc. thesis, Univ. of Ky.).

Other Records (items 17 and 19 are referable to collections 4 and 8).

15. Andre Michaux (1803) briefly noted *T. reflexum* from Kentucky.

16. Riddell (1835) also listed it, from "Dry hills, Ky."

17. Hussey (1876): "*Trifolium reflexum* occurs in several localities between the railroad and Mammoth Cave, which is in the eastern part of Edmonson County. I mention it because I have never found so many specimens in any one locality before, and also to make a note of the fine rose-pink color it everywhere had." But one label says "yellow".

18. Linney (1880, 1882) listed *T. reflexum*, along with *T. repens* and other exotics, from the southern Knobs or Bluegrass Regions.

19. Garman (1902): "It has not often been encountered growing wild in Kentucky. A specimen was sent me from Greenville, Muhlenberg County, June 8, 1897, by Mr. J. W. Barkley [see item 8]. It was observed on the place of Downer and Brother at Guthrie [Todd Co.], July 31, 1901."

20. It has been reported from Livingston Co. (R. Athey, pers. comm.).

We have found no report of any clover in the extensive pre-1850 literature on the Big Barrens in west-central Kentucky, as also reviewed by Baskin and Baskin (1981, and pers. comm.).

NOTES ON CULTIVATION AND CHROMOSOME NUMBERS

Our cultivation of *Trifolium stoloniferum* and *T. reflexum* has been mostly for propagation, with no experimental work completed yet, but the following observations have some value for future research. We have grown one clone of *T. stoloniferum* from the site discovered by Bartgis (1985) in Fayette County, WV, and have

started to grow material from the site in Boone County, KY. We have grown several accessions of *T. reflexum* from Kentucky and elsewhere.

1. If seed coats are scarified with emery paper, both species have good germination, i.e., 90 100% in a week on moist filter paper. Unscarified seed of *T. stoloniferum* has little or no germination, even after overwintering on moist soil in an unheated greenhouse; observations are continuing (C. Baskin, pers. comm.).

2. *T. stoloniferum* is easy to grow on moist, fertile soil without competition. Stolons can grow at least 70 cm in one season, rooting at nodes in contact with soil, which can be cut for easy propagation. Stolon growth is most vigorous during flowering in April to June, and it slows during warmer, drier weather. Each node can also develop short rhizomes that grow up to 5 cm long and 1 cm thick in three years. The plants from Kentucky appear more vigorous and tap-rooted than those from West Virginia. *T. reflexum* grows slower. It is typically a biennial, or winter annual if seed germinates in late summer; greenhouse plants, however, may persist into a third year if flowering is not stimulated by cold (see 8).

3. Judging from its native habitat and some trial plantings, *T. stoloniferum* does best in partial shade. Even with frequent watering and weeding, which is essential, plants in full sun appear to suffer from summer heat. Weeding of competitors is necessary even in partial shade. *T. reflexum* also seems to do best with a little shade.

4. We have not found rhizobial infections on the roots of *T. stoloniferum* from Kentucky or West Virginia. Attempts to infect it with rhizobial inoculum isolated from *T. reflexum* (Burton and Martinez 1960) produced only a few small uninfected nodules.

5. Some transplants of *T. stoloniferum* in open field conditions have become infected with "peanut stunt", a virus commonly infecting *T. pratense* and *T. repens* (S. A. Ghabriel, pers. comm.).

6. A powdery mildew often infects wild and cultivated *T. stoloniferum,* but it has little or no effect on growth. The fungus can be lost temporarily after winter freezes, and by propagation through seed.

7. *T. stoloniferum* appears relatively palatable to generalist herbivores, judging from frequent problems with slugs, voles, muskrats, rabbits, horses, etc. Attempts at establishment in some gardens failed completely due to rabbits (e.g., W. Davis, 1987, Ky. Native Plant Soc. Newsletter 2(3): 10).

8. Flowering of *T. stoloniferum* requires prior exposure to

temperatures of 30 40°C or less. In *T. reflexum,* some flowering occurs without such vernalization, but more flowering occurs with it. On favorable sites, both species have good seed production, even when self-pollinated. A well-developed head, with 20-40 flowers, generally produces at least 10 20 seeds. At least 100-200 seeds can be produced by one square meter of *T. stoloniferum*

9. We have determined the chromosome number of *T. stoloniferum* to be $2n = 16$, the same as *T. reflexum* (Wexelsen, 1928) and other native species in eastern North America (Cleveland, 1985).

DISCUSSION

Identity of the "Clover" in Early Accounts of the Bluegrass Region

The following points, together, strongly suggest that early notes of "clover" in the Bluegrass region refer to *Trifolium stoloniferum.*

a. The several references to "buffalo" or "native" clover suggest a native species. The region was called "the land of cane and clover" by Girty (see item 18 above), in describing the presettlement condition.

b. The accounts date from 1773 to 1792, when settlement was just beginning. "Clover" was apparently common in woodland with native plants, except perhaps for "bluegrass" (*Poa pratensis* L. may not be native). In these and other known accounts of the original ground vegetation on rich limestone soil (J. Campbell, unpublished), "clover" and "cane" are mentioned in 13 and 12 cases, respectively, followed by "peavine" (9 cases), "wild rye" (8 cases), "buffalo grass," "bluegrass," "nettle" (6 cases each) and other names.

c. We have observed that *T. stoloniferum* prefers partial shade, while exotics like *T. repens* prefer more open ground. Pursh (1816) observed that *T. repens* "makes its appearance wherever lands are cleared of timber, in the most remote parts of the country. . . on new plantations, from 60–100 miles distant. . ." *T. repens* probably spread in the Bluegrass region after the 1770s, but it is unlikely to have been frequent in the woodland before clearance.

d. Some accounts (13, 14, 23) suggest a more robust plant than typical *T. repens.* The large 'Landino' cultivar of *T. repens* had not been introduced then.

e. Some accounts (8, 10, 17) give flowering dates, ranging from late March to late May, according with the early flowering *T. stoloniferum.*

f. *T. stoloniferum* is the only native species collected within the

region; *T. reflexum* was collected to the north and west.

g. Some accounts refer to "white clover"; *T. reflexum* is usually reddish, always so in our experience.

h. The name "buffalo clover" need not just refer to *T. reflexum,* as in modern Floras, which distinguish *T. stoloniferum* as "running buffalo clover". There are no references to "running" before the Latin binomial of 1813. Any clover associated with buffalo could have been called "buffalo clover" by pioneers. An 1835 collection of *T. stoloniferum* was annotated "buffalo clover" (item 2, see also 23).

i. Based on notes in Floras throughout its range, *T. reflexum* generally occurs in rather dry regions, with *Pinus, Quercus* and *Carya,* not moist, rich woodlands of *Acer saccharum* and other trees that typified the Bluegrass Region before settlement (see next section).

j. It is unlikely that "clover" referred to another genus. In Kentucky, the "prairie-clovers", *Dalea (Petalostemum)* spp., are restricted to a few prairie remnants dominated by Andropogoneae. There is no evidence that such vegetation occurred within the Bluegrass Region. The "bush-clovers", *Lespedeza* spp., are virtually absent from richer Bluegrass soils, despite their abundance in disturbed areas elsewhere. The exotic "sweet clovers", *Melilotus* spp., are restricted to open disturbed sites, unlike the woodland described above.

After 1800, there are further references to "clover" or "white clover" in descriptions of the Bluegrass Region, but not as part of the natural vegetation. Most of the natural ground vegetation became highly disturbed by livestock and clearance. These later references suggest the introduced *Trifolium repens,* often in association with *Poa pratensis,* as part of the "woodland-pasture" that was more or less intentionally opened up by farmers. The only account suggesting *T. stoloniferum* after 1797 is Perrin's of 1882 (item 23 above), when it had apparently become uncommon and restricted to forest remnants.

Ranges and Habitats

The two native species in Kentucky probably overlapped little in range and habitat. Our data suggest that *Trifolium stoloniferum* was frequent in the Inner Bluegrass Region (Figure 1), and, further north, it occurred along the Ohio River (Boone County and probably Mason). North of the river, it also occurred on relatively moist and fertile areas of southern Ohio and southeastern Indiana, in the transition from the Outer Bluegrass Region to the Glaciated

Plains (Brooks 1983; see also Gist 1751, in Johnston, 1898; Smith 1795, in Morrow, 1907; David 1819; Finley 1853). There are no indications of *T. stoloniferum* from the poorer soils of the Eden Shale Belt, even though buffalo frequented areas like the Blue Licks, which had distinctive vegetation (Baskin & Baskin, 1985). Most records of *Trifolium reflexum* come from the former Big Barrens Region (Figure 2), which was covered by large areas of prairie-like grassland maintained by fire (Baskin & Baskin, 1981). There are no records of *T. reflexum* from the Bluegrass Region proper (on Ordovician bedrock), though it may have occurred on banks of the Ohio River and its tributaries (items 2, 3). We have no records of these species growing together anywhere.

The early accounts suggest that the typical vegetation containing *Trifolium stoloniferum* was woodland, with *Acer saccharum* (including *Acer nigrum* Michx. f.), *Fraxinus* spp., *Ulmus* spp., *Juglans nigra* L., *Gleditsia triacanthos* L., *Robinia pseudoacacia* L., *Morus rubra* L., *Celtis occidentalis* L., and relatively little *Quercus* and *Carya*. Such composition is typical of woodland remnants in the Inner Bluegrass today (J. Campbell, 1980, Ph.D. diss., Univ. of Ky.). The original ground vegetation, now greatly modified, appears to have been dominated by Gramineae, Leguminosae and Urticaceae, including *Elymus* spp. (wild rye), *Poa* spp. (bluegrass), perhaps *Panicum clandestinum* L. (buffalo-grass?), *Arundinaria gigantea* (cane), *Amphicarpaea bracteata* (pea-vine), *Urtica* spp. or *Laportea canadensis* (L.) Wedd. (nettles), and *Pilea pumila* (L.) Gray (rich-weed). The denser canebreaks probably contained little *T. stoloniferum*, as suggested by the more detailed descriptions above (especially 11 and 19). Cane is completely absent in accounts from the Ohio Valley to the north.

We have no historical accounts of the vegetation with *Trifolium reflexum*. However, the regions where it occurred generally have some kind of *Quercus-Carya* forest as the climax vegetation, and the original grasslands were dominated by Andropogoneae *(Andropogon, Schizachyrium, Sorghastrum),* in contrast to the grasses associated with *T. stoloniferum*. Thus, the two clover species appear to have been segregated along one of the major natural vegetation gradients in Kentucky, from *Acer saccharum* to *Quercus-Carya* forest (Campbell, 1987), and from C3 to C4 species among the dominant grasses (J. Campbell, unpub.). This shift in composition may be largely caused by greater moisture-stress and lower soil fertility.

Geographic and edaphic segregation extends to other native *Trifolium* species in eastern North America. *T. virginicum* Small is restricted to the shale barrens of West Virginia, Virginia, Maryland and Pennsylvania. An undescribed species (Leo Collins, Tennessee Valley Authority, Norris, TN, pers. comm.) is known only from cedar glades on Ordovician limestone in central Tennessee (one site) and western Virginia (two sites). *T. carolinianum* Michx. mostly occurs in openings within the *Quercus-Pinus* region on the Coastal Plain. Probably none of these species can survive indefinitely in undisturbed forest, and all may require some interruption of competing ground vegetation by disturbance or rock outcrops.

Possible Relationship with Buffalo and other Disturbance

We suggest that native clovers in Kentucky were formerly associated with trails and grassy areas in woods or savannas maintained by Indians or large herbivores buffalo, elk and deer. This hypothesis is supported by the following observations.

a. Both species were known as "buffalo clover" (see above).

b. Records of *Trifolium stoloniferum* and *T. reflexum* in Kentucky are mostly from the two major regions with evidence of pre-settlement disturbance by Indians or buffalo the Bluegrass and the Big Barrens.

c. Several early accounts indicate a close association between *T. stoloniferum* and "buffalo roads" or Indian trails (especially items 8, 10, 13, 14 and 22 above). Similar evidence exists in West Virginia (Bartgis, 1985) and Indiana (M. Homoya, pers. comm.). We have much less information on the original habitat of *T. reflexum* in Kentucky, though one of Short's collections (1825 45) says "fields and roadsides among the barrens" (item 1 above).

d. The known sites with well-established wild populations of *T. stoloniferum* are mostly on moist, fertile soils in woods along trails of some kind: at the edge of a dirt road (West Virginia); along a foot-path mowed annually (Kentucky); and in ravines with small terraces grazed by cattle (Indiana). Recent records of *T. reflexum* in and around Kentucky indicate similar disturbance: the Kentucky sites are along roads through woods or at edges (see above); the only site in Indiana is along a 10 15 year old logging trail through woods (M. Homoya, pers. comm.); and the most recent collection in Tennessee was from a "shaded roadbank" (F. W. Chester, pers. comm.). In floras, the habitat of *T. reflexum* in its northern range has been described in various ways, but usually indicating some association with disturbed woods or edges, often at roadsides.

e. From our experience with cultivation, it is clear that these species can become easily overtopped and outcompeted by taller plants, which must have been periodically removed by disturbance, such as grazing and trampling, in their original native habitat.

Hypotheses to Explain the Decline of Native Clovers

If these species were widespread along trails made by Indians and animals, why have they declined so much in Kentucky and elsewhere? (See figures 1, 2.) We suggest the following hypothetical factors, which are mostly ecological changes caused by human settlement.

a. Initial habitat destruction. Pioneers in the Ohio Valley Region generally followed pre-existing trails (Jakle, 1968), widening them and creating an excessively open and disturbed habitat. In contrast, trails with native clover that were not developed generally became too shady for the clovers, because Indian and large herbivore populations were reduced. Modern roads and trails freshly created in the woods may be suitable habitats, but there has been little undisturbed historical continuity with presettlement trails.

b. Poor dispersal to new habitat from remnant populations. After settlement, the potential for long-distance seed dispersal in the gut or hair of large herbivores has been greatly reduced.

c. Loss of natural grazing regime. Occasional heavy trampling and dung from buffalo and elk may have been important for promoting the native clovers relative to their competitors, just as cattle promote *T. repens* in pastures (Burdon, 1983). However, the typical high stocking rate for cattle, with no seasonal relief, causes excessive damage to the native clovers.

d. Increased consumer pressure (in addition to cattle). The apparent high palatability of *T. stoloniferum* (see Notes on Cultivation) deserves study in relation to possible increases of herbivores such as rabbits since settlement. Plants generally show no serious disease symptoms, but this point should be examined further, especially the virus infection in field-grown plants (see above).

e. Competition from exotic plants. Several Old World plants are common in disturbed woods and along trails, such as *Alliaria officinalis* L., *Glecoma hederacea* L., *Lonicera japonica* Thunb. and *Eulalia viminea* (Trin.) Kuntze. In open fields, many other exotics are abundant, including several *Trifolium* species, and these may further restrict the native *Trifolium* species to shady sites.

f. Reduced fire frequency. Fire, formerly set by Indians in some regions but now suppressed, may have promoted these species rela-

tive to their competitors. The Big Barrens, where some *T. reflexum* occurred, were largely maintained by fire before settlement, and fire has been important in states further south and west, where *T. reflexum* remains more frequent. However, there is no evidence that fire was important in the moister Bluegrass Region, with *T. stoloniferum.*

g. Lack of rhizobial infection in *T. stoloniferum.* This observation does not appear to reduce growth of cultivated plants seriously, if at all, but it should be studied further. Has a specific rhizobial genotype been lost? Search for rhizobia deserves high priority.

These hypotheses will be difficult to test. The most useful approach for conservation will be to begin trial plantings in habitats that approximate the presettlement condition, with careful comparative monitoring of successes and failures. Clearly, some disturbance by trampling, grazing or mowing is required. However, it may take some time to define the viable range of soil conditions, plant competitors and animal effects. The results may not show directly why the native clovers have declined, but they would probably be suggestive, and they would be of great practical importance for restoration in at least semi-natural environments.

Experimental work is also needed on the physiological differences between species, and on the population dynamics. For example, we do not yet know if the species differ in shade tolerance, and what causes the apparent differences in soil relationships, with absence of rhizobia in *Trifolium stoloniferum.* The more perennial habit, fewer flowering heads per ramet and larger seeds of *T. stoloniferum* suggest that it may produce fewer seeds than *T. reflexum,* making dispersal to new sites less likely. Dispersal biology itself is a difficult subject, especially within the context of landscape changes, but at least it might be relatively easy to ascertain if some seed can be carried through a buffalo's gut.

ACKNOWLEDGMENTS

We are particularly grateful to Rodney Bartgis for showing us *Trifolium stoloniferum* in West Virginia, and allowing us to take a piece for propagation, and to Mike Homoya for showing us the sites in Indiana. For information about native clovers elsewhere in eastern North America, we thank Ralph Brooks, Wayne Chester, Leo Collins, Alison Cusick, Robert Kral, Duane Isely, Sidney McDaniel, Donna Ware, Tom Wieboldt and Eugene Wofford. We also thank Carol and Jerry Baskin, Hal Bryan and Wayne Davis for

sharing their experiences with cultivation. Some expenses were paid by a grant to J. J. N. C. and N. L. T. from the Plant Conservation Center (Missouri Botanical Garden).

LITERATURE CITED

BARTGIS, R. L. 1985. Rediscovery of *Trifolium stoloniferum* Muhl. *ex* A. Eaton. Rhodora 87: 425–429.

BASKIN, J. M., AND C. C. BASKIN. 1981. The Big Barrens of Kentucky not a part of Transeau's Prairie Peninsula. *In:* R. L. Stuckey and K. J. Reese, Eds., The Prairie Peninsula—in the "Shadow" of Transeau. Proceeding of the 6th North American Prairie Conference, Columbus, Ohio, 12–17 Aug. 1978. Ohio Biol. Surv. Notes 15, p. 43–48.

BASKIN, C. C. AND J. M. BASKIN. 1985. A floristic study of a cedar glade in Blue Licks Battlefield State Park. Castanea 50: 19–25.

BRAUN, E. L. 1950. Deciduous Forests of Eastern North America. Blakiston Publishing Company, Philadelphia.

BROOKS, R. E. 1983. *Trifolium stoloniferum,* running buffalo clover: description, distribution, and current status. Rhodora 85: 343–354.

BRYANT, W. S., M. E. WHARTON, W. H. MARTIN AND J. B. VARNER. 1980. The Blue Ash-Oak Savanna-Woodland, a remnant of presettlement vegetation in the Inner Bluegrass of Kentucky. Castanea 45: 149–165.

BURDON, J. J. 1983. Biological Flora of the British Isles: *Trifolium repens* L. J. Ecol. 71: 307–330.

BURTON, J. C., AND C. J. MARTINEZ. 1960. Rhizobia inoculants for various leguminous species. Tech. Bull. Nitrogen Co, Milwaukee, Wisc. 101, p. 1–5.

CAMPBELL, J. J. N. 1987. Gradients of tree species composition in the Central Hardwood Region. *In:* R. L. Hay, F. W. Woods and H. DeSelm, Eds., Proceedings of the 6th Central Hardwood Forest Conference, Knoxville, Tennessee, 24–26 Feb. 1987, p. 325–346.

CLEVELAND, R. W. 1985. Reproductive cycle and cytogenetics. *In:* N. L. Taylor, Ed., Clover Science and Technology. Am. Soc. Agron. Monogr. 25: 71–110.

CRESSWELL, N. 1925. The Journal of Nicholas Cresswell, 1774–1777. Jonathan Cape, Ltd., London.

DAVID, T. 1819. Travels through the Western Country in the Summer of 1816. David Rumsey, Auburn, New York.

DORRIS, J. T., Ed. 1932. The Early History of Madison County by William Chenault. Register of Kentucky St. Hist. Soc. 30; 119–161.

EATON, A. 1818. Manual of Botany for the Northern and Middle States, 2nd ed. Webster & Skinners, Albany, New York.

FILSON, J. 1784. The Discovery, Settlement and Present Site of Kentucke. James Adams, Printer, Wilmington. (Also in Imlay, 1792).

FINLEY, J. B. 1853. Autobiography. Cranston and Curtis, Cincinnati.

GARMAN, H. 1902. Kentucky Forage Plants—the Clovers and their Allies. Kentucky Agric. Exp. Sta. Bull. No. 98.

HANNA, C. A. (Ed.) 1911. Lyman C. Draper's Account of John Finley, from his unfinished Life of Daniel Boone. *In:* The Wilderness Trail 2: 215–227. G. P. Putnams' Sons, New York.

HARRIS, E. 1928. Letter written in 1928. Filson Club Hist. Quart. 2: 165–166.

HUSSEY, J. 1876. Report on the Botany of Barren and Edmonson Counties. Rep. Geol. Surv. KY, 2nd Ser., 1: 34–58.

IMLAY, G. 1792. A Topographical Description of the Western Territory North America, 3rd ed. J. Debrett, London. (Reprinted by Augustus M. Kelley, New York.)

ISELY, D. 1951. The Leguminosae of the North Central United States. I. Loteae and Trifolieae. Iowa St. Coll. J. Sci. 25: 475.

JAKLE, J. A. 1968. The American Bison and Human Occupance of the Ohio Valley. Proc. Am. Phil. Soc. 112: 299 -305.

JILLSON, W. R. 1934. Pioneer Kentucky. The State Journal Company, Frankfort, Kentucky.

JOHNSTON, J. S. (Ed.). 1898. First Explorations of Kentucky. Filson Club Publ. 13. J. P. Morton and Co., Louisville, Kentucky.

KENTON, E. 1930. Simon Kenton: his Life and Period, 1755 1836. Doubleday, Doran and Company, New York.

LINNAEUS, C. 1753. Species Plantarum. Salvius, Stockholm.

LINNEY, W. M. 1880. Report on the Timbers of Boyle and Mercer County. Misc. Rep. Geol. Surv. Kentucky.

_____. 1882. Report on the Botany of Madison, Lincoln, Garrard, Washington and Marion Counties. Misc. Rep. Geol. Surv. Kentucky.

MARSHALL, H. 1812. The History of Kentucky. Volume I. Henry Gore, Frankfort, Kentucky.

MCAFEE, R. 1927. The Life and Times of Robert B. McAfee and his Family and Connections (1845). Register of Kentucky St. Hist. Soc. 25: 113–114.

MICHAUX, A. 1803. Flora Boreali-Americana 2: 59. C. Crapelet, Paris.

MORROW, J. (Ed.) 1907. Journals of J. F. D. Smith, 1783, 1795, 1797. Ohio Arch. Hist. Soc. Publ. 16: 371 399.

MORSE, J. 1789. The American Geography. Shepherd Kollock, Printer, Elizabethtown, New Jersey.

NELSON, J. C. 1919. Plants from Boone County, Kentucky. Proc. Indiana Acad. Sci. (1918), p. 125–143.

NOURSE, J. 1925. Journey to Kentucky in 1775. J. Am. Hist. 19: 251–260.

PERRIN, W. H. 1882. History of Fayette County, Kentucky. O. L. Baskin and Company, Chicago.

PURSH, F. T. 1816. Flora Americae Septentrionalis. James Black and Son, London.

RANCK, G. W. (Ed.) 1901. Boonesborough, Filson Club Publ. 16. J. P. Morton and Co., Louisville, Kentucky.

RIDDELL, J. L. 1835. Synopsis of the Flora of the Western States. E. Deming, Cincinnati.

SCHWAAB, E. L., Ed. 1973. Travels in the Old South. University of Kentucky Press, Lexington.

SMITH, J. G. 1896. Fodder and forage plants, exclusive of the grasses. U.S.D.A. Div. Agrost. Bull. 2.

STEYERMARK, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames.

THWAITES, R. G., AND L. P. KELLOGG, Eds. 1905. Documentary History of Dunmore's War 1774. Wisconsin Historical Society. Democrat Printing Company, Madison. (Also in L. C. Draper's Manuscripts, Wisc. Hist. Soc., 15CC: 157–162.

TOWNSEND, J. W., Ed. 1932. John Bradford's Historical &c. Notes on Kentucky. First printed in the Kentucky Gazette, 1826–27. Grabhorn Press, San Francisco.

U.S.D.A. SOIL CONSERVATION SERVICE. 1975. General Soil Map of Kentucky. Map No. 4-R-34874.

U.S. FISH AND WILDLIFE SERVICE. 1987. Endangered and threatened wildlife and plants; determination of endangered status for *Trifolium stoloniferum* (Running Buffalo Clover). Federal Register 52: 21478 21480.

WEXELSON, H. 1928. Chromosome number and morphology in *Trifolium*. University of California Publications in Agricultural Science 2: 355–376.

WOODS, N. M., Ed. 1905. The Woods-McAfee Memorial. Courier-Journal Job Printing Company, Louisville, Kentucky.

J. J. N. C.
SCHOOL OF BIOLOGICAL SCIENCES
UNIVERISTY OF KENTUCKY
LEXINGTON, KY 40506

M. E.
KENTUCKY NATURE PRESERVES COMMISSION
407 BROADWAY
FRANKFORT, KY 40601

M. E. M.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF LOUISVILLE
LOUISVILLE, KY 40292

N. L. T.
DEPARTMENT OF AGRONOMY
UNIVERSITY OF KENTUCKY
LEXINGTON, KY 40546

RHODORA, Vol. 90, No. 864, 1988

A SURVEY OF THE BENTHIC MARINE ALGAE OF SOUTHWESTERN NEW BRUNSWICK, CANADA

G. R. South, I. Tittley, W. F. Farnham and D. W. Keats

ABSTRACT

Southwestern New Brunswick, including the Passamaquoddy Bay area, is located in one of the richest marine environments in North America. A concentrated algal survey of this area comprising 50 littoral and sublittoral sites was undertaken in July 1986. Habitats investigated included estuaries, saltmarshes, saline lakes, sheltered and wave-exposed rocky shores, sublittoral bedrock, sediment and animal substrata.

A species-poor flora was recorded, comprising 171 algae (45 Chlorophyceae, 58 Phaeophyceae and 68 Rhodophyceae) out of 352 species known for eastern Canada. Five species new to eastern Canada were detected: (*Callocolax neglectus*, *Hildenbrandia crouanii*, *Phyllophora crispa*, *Sphacelaria caespitula* and *Chaetomorpha capillaris*). The *Halicystis ovalis* gametophyte phase of *Derbesia marina* was also recorded for the first time. The paucity of algal species in the Passamaquoddy region was probably due to regional conditions (low sea temperatures: 8°C offshore, 11°C inshore) and/or local conditions (littoral blanketing by *Ascophyllum nodosum*, sublittoral grazing by *Strongylocentrotus droebachiensis*).

Key Words: Survey, benthic marine algae, southern New Brunswick

INTRODUCTION

Southwestern New Brunswick, representative of the outer regions of the Bay of Fundy, is at the southernmost boundary of eastern Canada and is located in one of the richest marine environments in northeastern North America (Thomas, 1983). St. Andrews, situated centrally in the region, has become a world-renowned centre for marine studies since the establishment of the Department of Fisheries and Oceans Biological Station in 1909, and the Huntsman Marine Laboratory (now known as the Huntsman Marine Science Centre) in 1969. Surprisingly, however, very few studies of the benthic marine algae have been conducted in the region, and none has been sufficiently detailed to allow a reasonably comprehensive cataloguing of the representative species.

Records of the benthic marine algae of southwestern New Brunswick were incorporated in the catalogue of Cardinal (1968), in the eastern Canadian checklist series (South and Cardinal, 1970; South 1976, 1984) and by South and Tittley (1986). Taylor (1957) included all the species known for the region. Among the earliest species lists

referring specifically to southwestern New Brunswick are those of Hay (1886, 1887a,b), Fowler (1901, 1902) and Klugh (1916). Klugh (1924) and Bell (1927) conducted ecological studies of algae in the vicinity of St. Andrews, and included species records, while Colinvaux listed species from Mascabin Point and Lepreau Ledges (1959) and the Bay of Fundy (1966a). Colinvaux (1966b) also gave information on the location of herbarium material accumulated by previous workers in the area. Blackler (unpubl.) circulated a list of species collected at localities in southwestern New Brunswick and elsewhere made in association with the 1959 International Botanical Congress.

Bell and MacFarlane (1933), MacFarlane and Milligan (1965) and Edelstein et al. (1970) discussed the distribution of benthic marine algae in the Bay of Fundy, and Linkletter et al. (1977) included benthic algae in their checklist of the marine fauna and flora of Grand Manan Island and Passamaquoddy Bay, listing some 96 species. The utility of their list is greatly reduced, however, by their use of outdated or incorrect nomenclature. The most comprehensive catalogues pertinent to southwestern New Brunswick are those of Hehre et al. (1970), Stone et al. (1970), and Wilson et al. (1979). Hehre et al. (1970) reported 91 taxa from South Wolf Island, 114 taxa were collected from 10 stations on Campobello Island (Stone et al., 1970) and 254 taxa were reported for the Bay of Fundy by Wilson et al. (1979), with seven of the 21 stations covered being located in southwestern New Brunswick. Finally, a survey, including 13 stations in southwestern New Brunswick, was carried out by Smith et al. (1978), detailing the distribution of species from a number of sites not visited by previous workers.

Thomas (1983) included detailed accounts of the biota and ecology of Passamaquoddy Bay, with considerable attention being paid to seaweed communities. There is not, however, any account of the species composition of the region *per se*. A modern compilation and survey of the benthic marine algae of southwestern New Brunswick is therefore lacking. Information from previous surveys is incomplete; insufficient representative stations have been worked, especially with the aid of SCUBA. In the present investigation we report on the results of a concentrated survey of the shores of southwestern New Brunswick, essentially dealing with the coastline of Charlotte County (Figure 1) and including the islands of the Quoddy Region, Grand Manan and Campobello. Included is a comprehensive listing of species from the survey and from all previous studies available to us.

Field Survey

Field studies were undertaken in late June and early July, 1986. The littoral and sublittoral vegetation was recorded by direct observations at fifty sites located both inshore and off-shore (Figure 1). At littoral sites species were listed and the shore level at which they occurred recorded. Sublittoral bands of vegetation were identified by eye during SCUBA diving. Physical environmental parameters noted during diving included overall depth range of observations, topography, substratum type and extent of sedimentation, sea temperature and visibility. Particular attention was paid to sea urchin grazing. Samples of algae and substratum were taken from each band and returned to the laboratory for identification. Vertical ranges of sublittoral bands were recorded with a depth gauge, and depths were corrected to Chart Datum Table 1. Salinities were measured using a refractometer. Underwater visibilities were on the whole low (1–3 m), due to turbidity and plankton blooms, and reached 6–8 m only at site 42. Inshore sea temperatures were 11°C, offshore temperatures were lower (8°C); a thermocline was detected below 7m at site 29.

Sites Investigated

Sites visited are shown in Figure 1. Depths worked at each sublittoral site (Table I) have been corrected with reference to Chart Datum.

RESULTS

The following list of species is arranged alphabetically, by division. Species marked by an asterisk (*) are from published reports for the southern Bay of Fundy including southern Nova Scotia and the Passamaquoddy Bay area; species found only by S. C. Lindstrom (1985–1986 collections) are listed as (S. C. L.); supplementary data for the southern Bay of Fundy are given. Nomenclature follows South and Tittley (1986).

Voucher specimens from the present survey are housed in the Atlantic Reference Centre (Huntsman Marine Science Centre) and at BM.

CHLOROPHYCEAE

Acrochaete repens N. Pringsh.

Wilson et al. (1979): rare, from southwestern Nova Scotia. Intertidal, in *Fucus*.

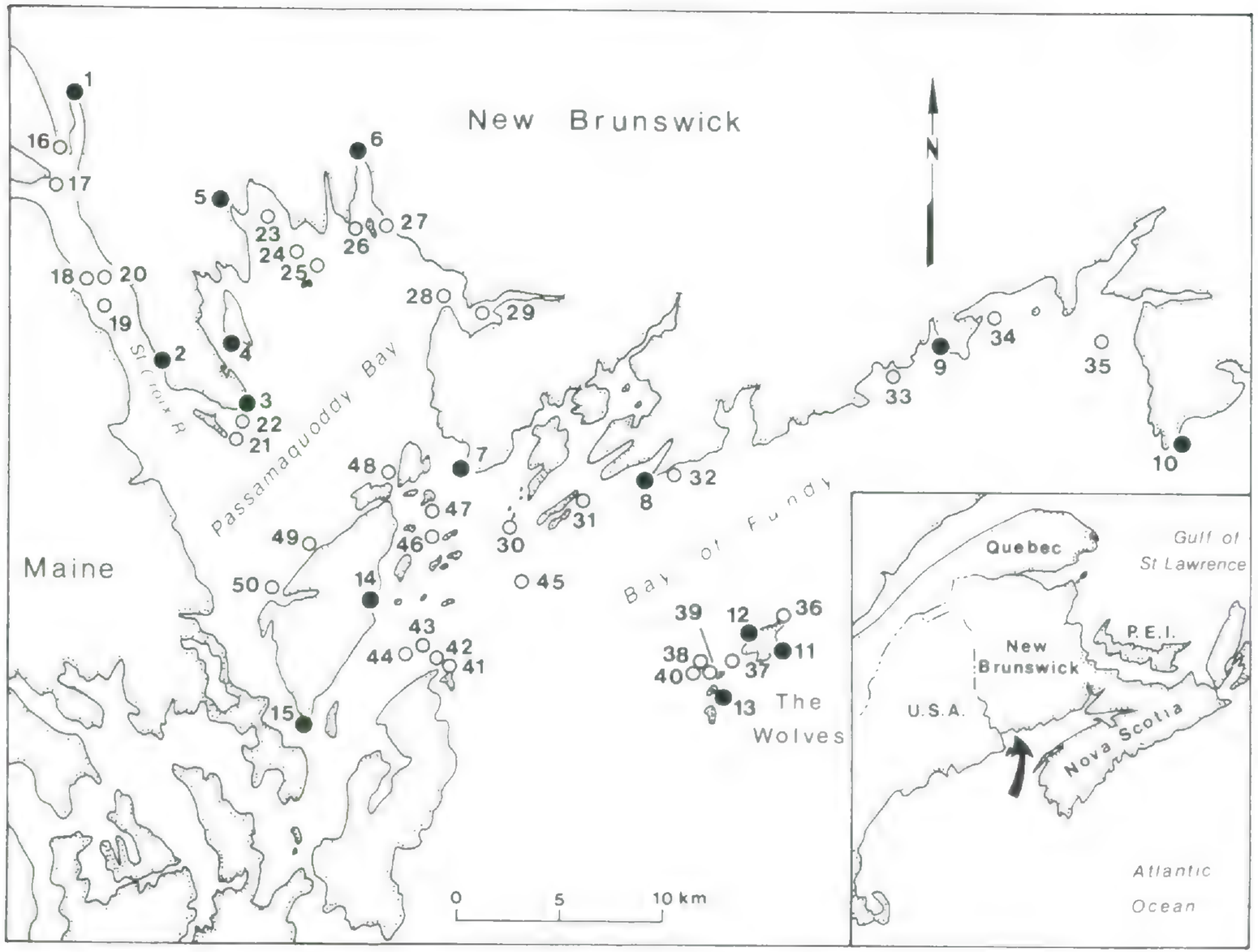


Figure 1. Map of southwestern New Brunswick, Canada (inset), showing the location of littoral (dark circles) and sublittoral (open circles) sampling stations, 1986.

A. viridis (Reinke) R. Nielsen
Littoral: brackish pool; epiphytic on *Polysiphonia*.
A. wittrockii (Wille) R. Nielsen
Lower littoral, sublittoral; endophytic; common
Blidingia marginata (J. Agardh) P. Dang.
Littoral: saltmarshes, on mud among *Spartina*: locally common.
B. minima (Naeg. ex Kuetz.) Kylin
Upper littoral; patchily band-forming; sporadic.
var. **ramifera** Bliding
In freshwater outfall.
Bolbocoleon piliferum N. Pringsh.
Littoral, sublittoral; endophytic in *Dumontia* and blades of *Agarum* and the seagrass *Zostera marina*.
Bryopsis hypnoides Lamouroux
Very rare, on rock in the lower littoral (S. C. L.)
***Capsosiphon fulvescens** (Agardh) Setch. et N. Gardn.
Wilson et al. (1979); rare but recorded from the Passamaquoddy area.
***C. groenlandicum** (J. Agardh) Vinograd.
Stone et al. (1970); Smith et al. (1978); Wilson et al. (1979).
Occasional, locally common.
***Chaetomorpha aerea** (Dillwyn) Kuetz.
Wilson et al. (1979); rare but recorded from the Passamaquoddy area.

Littoral Stations (1–15). **1.** Waweig Estuary; **2.** Brandy Cove; 3. Indian Point; **4.** Minister's Island; **5.** Sam Orr's Pond; **6.** Digdeguash Estuary; **7.** Mascabin Point; **8.** Pea Point; **9.** Crow Harbour; **10.** Pt. Lepreau; **11.** Southwest Cove, East Wolf Island; **12.** Paul's Cove, East Wolf Island; **13.** South Wolf Island; **14.** Northwest Harbour, Deer Island; **15.** Ferry Terminal, Deer Island.

Sublittoral Stations (16–50). ST. CROIX ESTUARY: **16.** North of Hill's Point; **17.** Hill's Point; **18.** St. Croix Island; **19.** Douchet's Island; **20.** Ross Point; **21.** Navy Island; **22.** Indian Point; PASSAMAQUODDY BAY: **23.** Hansen Point; **24.** Creighton Point; **25.** Hardwood Island; **26.** Hog Island, north corner; **27.** Oven Head; **28.** Magaguadavic Estuary, Midjik Bluff; **29.** Magaguadavic Estuary, opposite Mascarene; BACK BAY - LETANG: **30.** Pain Island (near White Head), Letite Passage; **31.** Green Island, Bliss Islands; PEA POINT - POINT LEPREAU: **32.** Pea Point by lighthouse; **33.** Between Seely's Cove and Crow Harbour; **34.** Red Head, Mace's Bay; **35.** The Brothers, Maces Bay, off Lepreau Ledges; THE WOLVES: **36.** East Wolf Island, NE end; **37.** Gull Rock; **38.** Fatpot Island; **39.** South Wolf Island, NW end; **40.** South Wolf Island, NE end; CAMPOBELLO ISLAND: **41.** Head Harbour; **42.** East Quoddy Head; **43.** Black Rocks; DEER ISLAND: **44.** South Sandy Island; **45.** White Horse Islet, SW side; **46.** Adam Island; **47.** Parker Island, SE side; **48.** Little Letite Passage, N. side of Mohawk Island; **49.** Davidson's Head; **50.** Gardner's Point.

Table 1. Sublittoral sites investigated (For locations, *see* Figure 1).

Locality Site No.	Site Name	Depth (m) (corrected to chart datum)
ST. CROIX ESTUARY[1]		
16.	North of Hills Point	0 to −6
17.	Hills Point	−1 to −9
18.	St. Croix Island, Inner End	+1 to −4
19.	Douchet's Island	+1 to −10
20.	Ross Point	0 to −4
21.	Navy Island	+2 to −2
PASSAMAQUODDY BAY[2]		
23.	Hansen Point	+4 to −5
24.	Creighton Point	+5 to −5
25.	Hardwood Island	+3 to −12
26.	Hog Island, north corner	−3 to −12
27.	Oven Head	−3 to −12
28.	Magaguadavic River estuary, Midjik Bluff	−1 to −6
29.	Magaguadavic River Estuary, opposite Mascarene	−2 to −11
BACK BAY - LETANG AREA[3]		
30.	Pain Island, (near White Head), Letite Passage	0 to −10
31.	Green Island, Bliss Islands	0 to −10
PEA POINT - POINT LEPREAU[4]		
32.	Pea Point by lighthouse	0 to −16
33.	Between Seely's Cove and Crow Harbour	+1 to −17
34.	Red Head, Maces Bay	+1 to −8
35.	The Brothers, Maces Bay, off Lepreau Ledges	+1 to −11
THE WOLVES[5]		
36.	East Wolf Island, northeast end	+1 to −14
37.	Gull Rock	0 to −14
38.	Fatpot Island	0 to −5
39.	South Wolf Island, northwest end	0 to −6
40.	South Wolf Island, northeast end	+1 to −8
CAMPOBELLO ISLAND[6]		
41.	Head Harbour	0 to −19
42.	East Quoddy Head	0 to −21
43.	Black Rocks	0 to −12

Table 1. Continued

Locality Site No.	Site Name	Depth (m) (corrected to chart datum)
DEER ISLAND[7]		
44.	South Sandy Island	0 to −13
45.	White Horse Islet, southwest side	+2 to −17
46.	Adam Island	+1 to −15
47.	Parker Island, southeastern side	+1 to −7
48.	Little Letite Passage, north side of Mohawk Island	+1 to −19
49.	Davidson's Head, Deer Island	+1 to −16
50.	Gardners Point, Deer Island	+1 to −4

1. Zone A in MacKay, 1978
2. Zone 1B in MacKay, 1978
3. Zone 2 in MacKay, 1978
4. Zone 6 in MacKay, 1978
5. Zone 5 in MacKay, 1978
6. Zone 3A in MacKay, 1978
7. Zone 3B in MacKay, 1978

C. brachygona Harvey

Upper littoral in pools; sporadic.

***C. cannabina** (Aresch.) Kjellman

Wilson et al. (1979): both sides of the Bay of Fundy.

C. capillaris (Kuetz.) Boerg.

Littoral; pools and shingle beach; sporadic. The status of this species is not clear (cf. Blair, 1983; South and Tittley, 1986).

C. linum (O. F. Muell.) Kuetz.

Midlittoral; rock pools; locally common. Estuaries, extensive mats in shallow standing water.

C. melagonium (F. Weber et Mohr) Kuetz.

Littoral, sublittoral (rare); rocks and pools; locally abundant. Once found abundantly in a deep pool in an estuary.

***C. piquotiana** Mont. ex Kuetz.

Smith et al. (1978); Grand Manan.

***Cladophora albida** (Hudson) Kuetz.

Wilson et al. (1979); rare but recorded from the Passamaquoddy area.

C. liniformis Kuetz.

Rare; forming loose-lying mats on littoral sand and mud in saltmarshes among phanerogams.

C. rupestris (L.) Kuetz.

Littoral; epilithic, rare.

C. sericea (Hudson) Kuetz.

Littoral, sublittoral; pools; locally common. Also found in estuarine saltmarshes and brackish pools.

Derbesia marina (Lyngbye) Solier

Sublittoral down to −15m; on sponges, especially *Isodictyon palmata* and *Halichondria* spp., *Boltenia* and other ascidians; locally common. *Halicystis ovalis*-phase epiphytic on crustose corallines at depths between −2 to −6m (gametes and zoospores on *Halicystis* and *Derbesia* phases, respectively).

Endophyton ramosa Gardner

Littoral; endophytic in *Chondrus crispus* (*see* Nielsen and McLachlan, 1986).

***Enteromorpha clathrata** (Roth) Grev.

Wilson et al. (1979); rare but recorded from the Passamaquoddy area.

E. compressa (L.) Grev.

Smith et al. (1978); Wilson et al. (1979); locally common.

E. flexuosa (Wulf. ex Roth) J. Agardh

Littoral; estuarine saltmarshes among *Spartina*; locally common.

subspecies **paradoxa** (Dillwyn) Bliding

Brackish habitats.

E. intestinalis (L.) Link

Upper littoral, shallow sublittoral; locally common in freshwater outfalls, brackish pools and estuarine saltmarsh.

E. linza (L.) J. Agardh

Littoral, shallow sublittoral; pools and draining water; locally common.

E. prolifera (O. F. Muell.) J. Agardh

Littoral; pools and draining water; locally common. Also in estuarine saltmarsh among *Spartina* and in brackish pools.

E. torta (Mert. in Juerg.) Reinb.

Littoral; freshwater seepage, brackish pools and estuarine saltmarsh among *Rhizoclonium* and *Spartina*; locally common.

Epicladia flustrae Reinke

Midlittoral; epizoic on obelioids and *Flustrella*; locally common.

Eugomontia sacculata Kornm.

Littoral, sublittoral down to −13m; open sea and estuarine saltmarsh; endozoic in shells (dead *Mytilus*, *Spisula*); locally common.

Gomontia polyrhiza (Lagerh.) Born. et Flah.

Littoral, sublittoral down to −13m; open sea and estuaries; endozoic in shells (*Spisula*; *Placopecten magellanicus*); locally common.

***Kornmannia leptoderma** (Kjellman) Kornm.

Stone et al. (1970); epiphytic on *Zostera* in summer. Wilson et al. (1979); rare but recorded from the Passamaquoddy area and southwestern Nova Scotia.

Monostroma grevillei (Thuret) Wittr.

Littoral; epilithic in pools and outfalls; locally common.

M. oxyspermum Kuetz.

Littoral, brackish pools.

***M. ? pulchrum** Farlow

Stone et al. (1970); abundant at lower littoral and sublittoral levels. Smith et al. (1978); Wilson et al. (1979); abundant throughout the Bay of Fundy.

Ochlochaete hystrix Thwaites ex Harvey

Littoral; brackish pools; epiphytic, uncommon.

Percursaria percursa (Agardh) Bory

Littoral; estuarine saltmarsh on mud among *Spartina*; brackish pools, uncommon.

***Pilinia ? endophytica** F. Collins

Wilson et al. (1979); rare, once in Nova Scotia.

P. ? lunatiae F. Collins

Rare, on shells.

Prasiola stipitata Suhr in Jessen

Littoral fringe; epilithic; locally common in bird roosts.

Prinsheimiella scutata** (Reinke) Hoehnel ex Marchew.

Littoral; epiphytic on *Phyllophora truncata*; locally common.

***Pseudendoclonium fucicola** (Rosenv.) R. Nielsen

Wilson et al. (1979); rare, coast of Nova Scotia.

P. submarinum Wille

Wilson et al. (1979); occasional but more frequent in the Passamaquoddy area.

***Pseudopringsheimia confluens** (Rosenv.) Wille

Wilson et al. (1979); rare, once in Nova Scotia.

Rhizoclonium riparium (Roth) Kuetz. ex Harvey

Littoral; rocky shores and estuarine saltmarsh among *Spartina*; locally common.

Rosenvingiella polyrhiza (Rosenv.) Silva

Littoral fringe; epilithic, rare, bird roosts.

Spongomorpha aeruginosa (L.) Hoek

Littoral, sublittoral; pilings, pools and rocks; common.

S. arcta (Dillwyn) Kuetz.

Littoral, upper sublittoral; epilithic; common

***S. sonderi** Kuetz.

Wilson et al. (1979); rare, Campobello Island and Nova Scotia.

S. spinescens Kuetz.

Littoral, sublittoral fringe in *Alaria* zone; lower shore pools; epilithic, common.

***Stichococcus marinus** (Wille) Hazen

Wilson et al. (1979); rare, Passamaquoddy area.

Ulothrix flacca (Dillwyn) Thuret in Le Jolis

Littoral, sublittoral; epilithic, epiphytic, epizoic; estuarine saltmarsh and freshwater seepage; common.

***U. laetevirens** (Kuetz.) F. Collins

Smith et al. (1978); Wilson et al. (1979); rare, Passamaquoddy area.

***U. speciosa** (Carmich. ex Harvey in Hook.) Kuetz.

Stone et al. (1978); upper midlittoral, epiphytic and epilithic. Wilson et al. (1979); locally common.

Ulva lactuca L.

Littoral, shallow sublittoral; rocky shore pools and estuaries; common.

***U. rigida** Agardh

Smith et al. (1978); Wilson et al. (1979); common throughout the Bay of Fundy.

Ulvaria obscura (Kuetz.) Gayral

Sublittoral down to −3m; epilithic, common.

var. **blyttii** (Aresch.) Bliding occurred in upper midlittoral pools and in estuaries near low water level; also sublittoral fringe.

Uronema ? curvata Printz

Sublittoral down to −14m; epiphytic on ? *Cruoria arctica*; rare.

Urospora penicilliformis (Roth) Aresch.

Sublittoral down to −9m; epilithic; uncommon.

U. wormskioldii (Mert. in Hornem.) Rosenv.
Stone et al. (1970); uncommon, epilithic, lower littoral. Smith et al. (1978): Grand Manan.

PHAEOPHYCEAE

***Acrothrix gracilis** Kylin
Wilson et al. (1979; as *A. novae-angliae*); rare, southwestern Nova Scotia.

Agarum cribrosum (Mert.) Bory
Lower littoral (pools), sublittoral down to −10m (mainly sporelings); epilithic; patchy or scattered plants. Some plants with galls.

Alaria esculenta (L.) Grev.
Lower littoral (pools), shallow sublittoral; epilithic; abundant in wave-exposed situations.

Ascophyllum nodosum (L.) Le Jolis
Littoral, epilithic; abundant, particularly in sheltered situations. Ecad **scorpioides** was locally common on stones in saltmarshes.

Asperococcus fistulosus (Hudson) Hook.
Littoral, sublittoral; epizoic on shells, epiphytic on sunken drift *Fucus*; rare but locally common.

***Chorda filum** (L.) Stackh.
Wilson et al. (1979); common, throughout the outer Bay of Fundy.

Chorda tomentosa Lyngbye
Sublittoral fringe; epilithic, common.

Chordaria flagelliformis (O. F. Muell.) Agardh
Littoral, sublittoral, epilithic, epiphytic on *Chondrus*; often in pools; common.

***Cladosiphon zosterae** (J.Agardh) Kylin
Stone et al. (1970); Wilson et al. (1979); common. Campobello Island and southwestern Nova Scotia.

***Coilodesme bulligera** Stroemf.
Wilson et al. (1979); rare, Nova Scotia.

***Colpomenia peregrina** Sauvageau
Wilson et al. (1979); rare, southwestern Nova Scotia.

Delamarea attenuata (Kjellman) Rosenv.
In upper tidepools, rare (S. C. L.)

Desmarestia aculeata (L.) Lamouroux

Lower littoral (pools), sublittoral fringe; epilithic; locally common.

D. viridis (O. F. Muell.) Lamouroux

Lower littoral (pools), sublittoral down to −5m; epilithic; abundant as large clumps in the shallow sublittoral.

Desmotrichum undulatum (J. Agardh) Reinke

Uncommon, epiphytic, lower littoral (S. C. L.)

***Dictyosiphon chordaria** Aresch.

Wilson et al. (1979); rare.

D. eckmanii Aresch.

Sublittoral; epilithic, epiphytic on *Petalonia*; rare but locally common.

D. foeniculaceus (Hudson) Grev.

Littoral, (?) sublittoral, epilithic, epiphytic on *Chordaria*; in pools, common.

***D. macounii** Farlow

Stone et al. (1970); found once in August. Wilson et al. (1979); rare, Campobello Island and Nova Scotia.

Ectocarpus fasciculatus Harvey

Littoral, sublittoral fringe; epilithic, epiphytic on various algae; common.

E. siliculosus (Dillwyn) Lyngbye

Sublittoral fringe; epilithic, epiphytic on *Scytosiphon* and *Laminaria*; open coast, estuaries and brackish pools; common.

***Elachista chondri** Aresch.

Wilson et al. (1979); rare, Point Lepreau only.

E. fucicola (Velley) Aresch.

Littoral; epiphytic on *Ascophyllum* and *Fucus*; common.

Endodictyon infestans Gran

Sublittoral; epiphytic/endophytic in/on *Agarum*; rare.

Eudesme virescens (Carmich. ex Harvey in Hook.) J. Agardh

Sublittoral down to −13m; epilithic; rare.

Fucus distichus L.

Upper littoral pools; epilithic; locally common.

Fucus evanescens Agardh

Littoral; epilithic; band-forming on lower shore rocks; common.

***F. serratus** L.

Wilson et al. (1979); introduced, southeastern Nova Scotia.

F. spiralis L.

Upper littoral; epilithic; band-forming; open coast and estuaries; common.

F. vesiculosus L.

Upper littoral; epilithic; open coast and estuaries; common.

Giffordia granulosa (Sm.) Hamel

Wilson et al. (1979); rare, Point Lepreau and Grand Manan.

G. ovata (Kjellman) Kylin

Rare, lower littoral, upper sublittoral.

***Halopteris scoparia** (L.) Sauvageau

Wilson et al. (1979); rare, Campobello Island and southwestern Nova Scotia.

Haplospora globosa Kjellman

Sublittoral; rare, Point Lepreau (Hooper, unpubl., in Herb., NFLD)

***Hecatonema ? reptans** (Kjellman) Sauvageau

Wilson et al. (1979); rare (taxonomic status uncertain).

Isthmoplea sphaerophora (Carmich. ex Harvey in Hook.) Kjellman

Littoral, shallow sublittoral; epiphytic on *Plumaria* and *Desmarestia aculeata*; sporadic.

Laminaria digitata (Hudson) Lamouroux

Lower littoral pools, sublittoral fringe; epilithic; band-forming; common.

L. longicruris Bach. Pyl.

Lower littoral; epilithic; occasional.

L. saccharina (L.) Lamouroux

Lower littoral pools, shallow sublittoral down to −4m; epilithic; common.

***Laminariocolax tomentosoides** (Farlow) Kylin

Wilson et al. (1979); rare, once in Nova Scotia.

Leathesia difformis (L.) Aresch.

Littoral; epiphytic on *Corallina*; rare.

Leptonematella fasciculata (Reinke) Silva

Low littoral, rocks (S. C. L.).

Melanosiphon intestinalis (Saund.) Wynne

Upper littoral; epilithic and on wood pilings; open coast and estuaries; common.

***Microspongium globosum** Reinke

Wilson et al. (1979); southwestern Nova Scotia.

***Mikrosyphar polysiphoniae** Kuck.

Wilson et al. (1979); rare, recorded only once in Nova Scotia.

***M. porphyrae** Kuck.

Wilson et al. (1979); rare, recorded only once in Nova Scotia.

M. zosterae Kuck.

Littoral; epiphytic on decaying *Spartina* leaves, saltmarsh; rare.

***Myriocladia lovenii** Agardh

Wilson et al. (1979); rare, southwestern Nova Scotia.

***Myrionema corunnae** Sauvageau

Wilson et al. (1979); rare, recorded only once in Nova Scotia.

***M. magnusii** (Sauvageau) Lois.

Wilson et al. (1979); rare, southwestern Nova Scotia, once.

M. strangulans Grev.

Littoral; epiphytic on *Ulva*; rare.

***Myriotrichia clavaeformis** Harvey

Wilson et al. (1979; as *M. filiformis*); rare.

Petalonia fascia (O. F. Muell.) O. Kuntze

Littoral pools, sublittoral fringe; epilithic, common.

***Petroderma maculiforme** (Wollny) Kuck.

Wilson et al. (1979); rare, southwestern Nova Scotia.

Pilayella littoralis (L.) Kjellman

Littoral, sublittoral; epilithic, epiphytic on various algae; estuaries, saltmarshes, brackish pools and open coast; common.

Pogotrichum filiforme Reinke

Sublittoral fringe; epiphytic on *Laminaria digitata*; uncommon.

Pseudolithoderma extensum (P. Crouan et H. Crouan) S. Lund

Sublittoral; epilithic and epizoic on scallop shells; uncommon.

Punctaria latifolia Grev.

Stone et al. (1970); epiphytic on *Zostera*. July and August. Wilson et al. (1979).

Ralfsia fungiformis (Gunnerus) Setch. et Gardn.

Lower littoral pools; epilithic, locally common.

***R. pusilla** (Stroemf.) Batters

Stone et al. (1970); rare, found once in October, epiphytic. Wilson et al. (1979); rare, recorded only once on Campobello Island.

R. verrucosa (Aresch.) J. Agardh

Littoral, sublittoral; epilithic, epizoic on shells; estuaries, brackish pools, open coast; locally common.

Saccorhiza dermatodea (Bach. Pyl.) J. Agardh

Lower littoral pools, shallow sublittoral; epilithic, especially on boulder tops; locally common.

***Scytosiphon dotyi** Wynne

Smith et al. (1978); Grand Manan. Wilson et al. (1979); occasional, throughout the Bay of Fundy.

S. lomentaria (Lyngbye) Link

Littoral pools, sublittoral fringe down to "2m; epilithic; estuaries and open coast.

Sorapion kjellmannii (Wille) Rosenv.

Littoral pools, sublittoral; epilithic, epizoic on shells; uncommon.

***Sphacelaria arctica** Harvey

Wilson et al. (1979); rare, recorded only once in Nova Scotia.

S. caespitula Lyngbye

Littoral; epilithic, uncommon.

S. cirrosa (Roth) Agardh

Shallow sublittoral; epilithic, uncommon.

S. fusca (Hudson) S. F. Gray

Rare, epilithic (S. C. L.)

S. nana Naeg. ex Kuetz.

Midlittoral; on shaded estuarine pilings; rare.

***S. plumosa** Lyngbye

Wilson et al. (1979); rare, southwestern Nova Scotia.

S. radicans (Dillwyn) Agardh

Lower littoral pools; epilithic, rare.

S. rigidula Kuetz.

Littoral; epiphytic on *Chondrus*; brackish pools, rare.

***Sphaerotrichia divaricata** (Agardh) Kylin

Wilson et al. (1979); occasional, throughout the Bay of Fundy.

Spongonema tomentosum (Hudson) Kuetz.

Widely distributed, uncommon (S. C. L.).

Stictyosiphon griffithsianus (Le Jolis) Holmes et Batters

Sublittoral; epiphytic on *Dictyosiphon foeniculaceus*; rare.

***S. soriferus** (Reinke) Rosenv.

Wilson et al. (1979); rare, southwestern Nova Scotia.

S. tortilis (Rupr.) Reinke

Sublittoral; epilithic, rare.

Stilophora rhizodes (Turner) J. Agardh

Lower littoral pools; epilithic; found only once.

Streblonema ? chordariae (Farlow) De Toni

Sublittoral; epizoic on hydroids and erect bryozoans; rare.

***S. ? effusum** Kylin

Wilson et al. (1979); rare, Nova Scotia.

S. oligosporum Stroemf.
Sublittoral fringe; endophytic in *Devaleraea*; see South (1984) regarding binomial.

S. parasiticum (Sauvageau) Levr.
Wilson et al. (1979); rare, once in Nova Scotia.

***S. polycladum** Jaasund
Wilson et al. (1979; as *Entonema polycladum*); rare, Nova Scotia.

Ulonema rhizophorum Foslie
Littoral; epiphytic on *Dumontia*; rare.

RHODOPHYCEAE

Ahnfeltia plicata (Hudson) Fries
Lower littoral; pools; epilithic; locally common.
Porphyrodiscus phase sublittoral, epilithic on quartz, rare.

***Antithamnion cruciatum** (Agardh) Naeg.
Smith et al. (1978) from Grand Manan. Stone et al. (1970); found only once in May, lower littoral. Wilson et al. (1979); both coasts of Fundy.

Antithamnionella floccosa (O. F. Muell.) Whitt.
Lower littoral, shallow sublittoral; pools; epiphytic on *Polysiphonia* and stipes of *Laminaria digitata*, epizoic on hydroids; uncommon.

***Audouinella alariae** (H. Jonss.) Woelk.
Wilson et al. (1979); rare.

A. daviesii (Dillwyn) Woelk.
Sublittoral; epiphytic on *Phycodrys*; rare.

A. membranacea (Magnus) Papenf.
Sublittoral down to −20m; epizoic on hydroids, bryozoa and the sponge *Isodictyon*: common.

***A. microscopica** (Naeg. in Kuetz.) Woelk.
Wilson et al. (1979); rare.

A. purpurea (Lightf.) Woelk.
Littoral, sublittoral, epilithic, epiphytic on *Laminaria digitata* stipes and epizoic on hydroids; common.

***A. saviana** (Menegh.) Woelk.
Wilson et al. (1979); rare, western Nova Scotia, Passamaquoddy Bay area.

A. secundata (Lyngbye) P. Dixon in Parke et P. Dixon
Littoral, sublittoral, epiphytic on many species of algae; common.

A. spetsbergensis (Kjellman) Woelk.
Sublittoral down to −3m; epizoic on hydroids (*Tubularia* spp.); common.

Bangia atropurpurea (Roth) Agardh
Locally common, spring and summer.

***Bonnemaisonia hamifera** Hariot
Wilson et al. (1979); rare, southwestern Nova Scotia.

***Callithamnion corymbosum** (Sm.) Lyngbye
Wilson et al. (1979); rare, western Nova Scotia, once in the inner Bay of Fundy.

***C. tetragonum** (With.) S. F. Gray
Wilson et al. (1979); rare, southwestern Nova Scotia.

Callocolax neglectus Schmitz ex Batters
Sublittoral down to −17m; parasitic on old plants of *Callophyllis cristata*; rare.

Callophyllis cristata (Agardh) Kuetz.
Lower littoral, sublittoral down to −20m; epilithic (particularly crevices and edges), epizoic on sponges, hydroids and *Boltenia* stalks; common.

Ceramium deslongchampii Chauvin in Duby
Lower littoral; epilithic, epiphytic on *Mytilus*; rare.

C. diaphanum (Lightf.) Roth
Littoral; (?) epilithic; rare.

C. elegans (Roth) Ducluz.
Littoral, epilithic, rare (S. C. L.).

C. rubrum (Hudson) Agardh
Littoral; epilithic; uncommon.

***C. strictum** Harvey
Wilson et al. (1979); rare, southwestern Nova Scotia, Point Lepreau.

Ceratocolax hartzii Rosenv.
Lower littoral; pools; parasitic on *Phyllophora*; rare.

***Champia parvula** (Agardh) Harvey
Wilson et al. (1979); rare, western Nova Scotia and near Grand Manan.

Chondrus crispus Stackh.
Littoral; common on rocks and in pools, band-forming at lower shore levels, also in brackish pools and estuaries; common.

Choreocolax polysiphoniae Reinsch
Wilson et al. (1979); rare, inner Bay of Fundy — Nova Scotia coast.

Clathromorphum circumscriptum (Stroemf.) Foslie

Lower littoral, sublittoral down to −15m; epilithic, epizoic on various shells, widespread but uncommon.

C. compactum (Kjellman) Foslie

Sublittoral down to −20m; epilithic usually on cobbles, epizoic on *Modiolus*, occasionally forming small rhodoliths; common, locally dominant.

"Conchocelis rosea" stage of *Porphyra* species.

Sublittoral; endozoic in shells (dead *Mytilus*); widespread.

Corallina officinalis L.

Littoral, shallow sublittoral; epilithic, common.

"Cruoriopsis hauckii" stage (see *Gloiosiphonia* below)

Sublittoral; small crusts on pebbles; rare.

Cystoclonium purpureum (Hudson) Batters

Lower littoral, sublittoral fringe; pools, epilithic, locally common.

***Dasya baillouviana** (S. Gmelin) Mont.

Wilson et al. (1979); rare, southwestern Nova Scotia.

Devaleraea ramentacea (L.) Guiry

Littoral, sublittoral fringe; rocks and pools, common.

Dumontia contorta (S. Gmelin) Ruprecht

Littoral, sublittoral fringe pools, estuarine standing water; epilithic; common.

Erythrotrichia carnea (Dillwyn) Agardh

Littoral, brackish pool; epiphytic on *Zostera*; locally abundant.

Erythrotrichopeltis ciliaris (Carmich. ex Harvey in Hook.) Kornm.

Sublittoral; epizoic on hydroids; rare.

***Fimbrifolium dichotomum** (Lepechin) G. Hansen

Smith et al. (1978); from Grand Manan. Wilson et al. (1979; as *Rhodophyllis dichotoma*); occasional, outer Bay of Fundy (both Nova Scotia and New Brunswick coasts).

***Fosliella farinosa** (Lamouroux) Howe

Wilson et al. (1979; as *Melobseia farinosa*); rare, Point Lepreau and southwestern Nova Scotia.

Gloiosiphonia capillaris (Hudson) Carmich. ex Berk.

Cruoriopsis hauckii stage (see above).

***Gymnogongrus crenulatus** (Turner) J. Agardh

Wilson et al. (1979); rare, Point Lepreau only.

Halosacciocolax kjellmani S. Lund

Littoral; epiphytic on *Palmaria*; rare.

Harveyella mirabilis (Reinsch) Reinke

Littoral; parasitic on *Rhodomela confervoides*; rare.

***Helmithora divaricata** (Agardh) J. Agardh
"**Audouinella polyides**" stage (cf. South and Tittley, 1986); Wilson et al. (1979; as *Colaconema polyides*); southwestern Nova Scotia.

Hildenbrandia crouanii J. Agardh
Littoral; sublittoral to −10m; epilithic on stones; open coast and estuaries; uncommon.

H. rubra (Sommerf.) Menegh.
Littoral, sublittoral; epilithic; open coast, estuaries and brackish pools; uncommon.

Kvaleya epilaeve Adey et Sperapani
Sublittoral; parasitic on *Leptophytum laeve*; rare. Our single record from site 19 requires confirmation but may represent the southern limit of distribution of this northern adeloparasite.

***Leptophytum foecundum** (Kjellman) Adey
Wilson et al. (1979); rare, location unspecified.

L. laeve (Stroemf.) Adey
Sublittoral, below −10m; epilithic, usually on pebbles; common.

***Lithophyllum orbiculatum** (Foslie) Foslie
Wilson et al. (1979); throughout Bay of Fundy.

Lithothamnion glaciale Kjellman
Sublittoral down to −20m; epilithic, epizoic on *Modiolus*; forms rhodoliths; locally common.

L. lemoineae Adey
Lower littoral, sublittoral down to −18m; epilithic, epizoic on shells, occasionally forms small rhodoliths.

***Lomentaria baileyana** (Harvey) Farlow
Wilson et al. (1979); rare.

***L. orcadensis** (Harvey) F. Collins ex W. Taylor
Wilson et al. (1979); rare, southwestern Nova Scotia.

Mastocarpus stellatus (Stackh. in With.) Guiry in Guiry, West, Kim et Masuda
Lower littoral; rocks and pools, often band-forming, common. *Petrocelis cruenta* (tetrasporic) phase detected.

***Melobesia membranacea** (Esper) Lamouroux
Wilson et al. (1979); rare, found once in Nova Scotia.

Membranoptera alata (Hudson) Stackh.
Littoral, sublittoral; epiphytic on *Agarum* and *Ptilota*, epizoic on hydroids; rare, mainly as sporelings.

***Odonthalia dentata** (L.) Lyngbye
Wilson et al. (1979); rare, Nova Scotia coast.

Palmaria palmata (L.) O. Kuntze

Littoral, sublittoral fringe; epilithic, often band-forming; abundant.

Pantoneura baerii (Postels et Rupr.) Kylin

Littoral pools; epiphytic; rare.

Peyssonnelia rosenvingii Schmitz in Rosenv.

Lower littoral, sublittoral down to −18m and more; epilithic, epiphytic on crustose corallines, epizoic on *Modiolus*; common. (Possibly recorded by Logan et al. (1983) as *Petrocelis middendorfii*).

Phycodrys rubens (L.) Batters

Pools, lower littoral, sublittoral; epiphytic, epilithic; common

Phyllophora crispa (Hudson) P. Dixon

Shallow sublittoral down to −2m; epilithic; rare (found only twice) but locally common.

P. pseudoceranoides (S. Gmelin) Newr. et A. Tayl.

Lower littoral; pools; epilithic; rare but locally common.

P. traillii Holmes *ex* Batters

Lower littoral; epilithic — shaded crevices.

P. truncata (Pallas) A. Zin.

Sublittoral fringe; epilithic; open coast and once in brackish pool; rare but locally common in clumps.

Phymatolithon laevigatum (Foslie) Foslie

Sublittoral to −15m; epilithic, generally on bedrock and large boulders; locally common.

***P. lendormanii** (Aresch. in J. Agardh) Adey

Wilson et al. (1979); common, on the coast of Nova Scotia.

P. rugulosum Adey

Sublittoral down to −18m; epilithic, usually on larger boulders, occasionally epizoic on shells, abundant.

***Platoma bairdii** (Farlow) Kuck.

Wilson et al. (1979); rare, recorded twice from New Brunswick.

Plumaria elegans (Bonnem.) Schmitz

Littoral, sublittoral fringe; epilithic, common.

***Pneophyllum lejolisii** (Rosan.) Chamberlain

Wilson et al. (1979; as *Melobesia lejolisii*); occasional, southwestern Nova Scotia.

Polyides rotundus (Hudson) Grev.

Lower littoral; epilithic; pools, locally common.

***Polysiphonia arctica** J. Agardh

Wilson et al. (1979); rare, Campobello Island.

***P. brodiaei** (Dillwyn) Sprengel
Wilson et al. (1979); rare, southwestern Nova Scotia.

P. elongata (Hudson) Sprengel
Intertidal; epilithic, rare.

P. fibrillosa (Dillwyn) Sprengel
Littoral; brackish pool; rare but locally common.

P. flexicaulis (Harvey) F. Collins
Littoral, epilithic; rare.

P. harveyi J. Bailey
Lower littoral pools, sublittoral down to −10m; epilithic; locally common.

P. lanosa (L.) Tandy
Littoral; epiphytic on *Ascophyllum*; common.

***P. nigrescens** (Hudson) Grev.
Wilson et al. (1979); occasional throughout the Bay of Fundy.

P. urceolata (Lightf. ex Dillwyn) Grev.
Littoral; sublittoral down to −17m; epilithic, epiphytic on various algae; abundant. Some plants showing swollen pericentral cells, perhaps as a result of fungal infection.

Porphyra leucosticta Thuret in Le Jolis
Littoral; epiphytic on *Fucus*; common.

P. linearis Grev.
Upper intertidal; epilithic, rare.

P. miniata (Agardh) Agardh
Lower littoral, sublittoral down to −10m; epilithic, epiphytic; common.

P. purpurea (Roth) Agardh
Littoral, sublittoral fringe; epilithic; occasional.

P. umbilicalis (L.) J. Agardh
Littoral, sublittoral fringe; epilithic, free-floating in pools; locally common.

***Porphyropsis coccinea** (J. Agardh ex Aresch.) Rosenv.
Wilson et al. (1979); rare, Grand Manan and once in Nova Scotia.

***Pterothamnion plumula** (Ellis) Naegeli
Wilson et al. (1979); southwestern Nova Scotia.

Ptilota serrata Kuetz.
Lower littoral, sublittoral down to −15m; epilithic, epizoic especially on *Boltenia*; common.

Rhodomela confervoides (Hudson) Silva
Littoral pools, shallow sublittoral; epilithic; common.

Rhodophysema elegans (P. Crouan et H. Crouan ex J. Agardh) P. Dixon

Sublittoral down to −10m; epilithic on quartz and glass; uncommon.

***R. georgii** Batters

Wilson et al. (1979); rare, Campobello Island and southwestern Nova Scotia.

Scagelia pylaisei (Mont.) Wynne

Sublittoral down to −20m; epilithic (rarely), epiphytic (commonly) on various algae, *Boltenia*, bryozoa and hydroids; common.

***Scinaia forcellata** Biv.

Wilson et al. (1979); rare, southwestern Nova Scotia.

***Spermothamnion repens** (Dillwyn) Rosenv.

Stone et al. (1970); found only once in June, epiphytic on *Polyides*. Wilson et al. (1979); Campobello Island.

***Spyridia filamentosa** (Wulf.) Harvey in Hook.

Wilson et al. (1979); rare, Grand Manan and western Nova Scotia.

Stylonema alsidii (Zanard.) Drew

Littoral, epiphtytic on *Sphacelaria rigidula*; brackish pool; rare.

***Titanoderma corallinae** (P. Crouan et H. Crouan) Woelk., Chamberlain et Silva

Wilson et al. (1979; as *Lithophyllum corallina*); rare, Campobello Island and southwestern Nova Scotia.

T. pustulatum (Lamouroux) Woelk., Chamberlain et Silva

Lower littoral; epiphytic on *Mastocarpus*; rare but locally common.

Turnerella pennyi (Harvey) Schmitz

Sublittoral down to −20m; epilithic (often in crevices), epiphytic on crustose corallines, epizoic on *Modiolous*; common. *Cruoria arctica*-phase also detected (rarely).

CYANOPHYCEAE

Aphanocapsa spp.

Shallow sublittoral; endozoic in sponges (*Halichondria* spp.); widespread.

***Calothrix crustacea** Thur. *ex* Bornet et Flah. as *Rivularia atra* Thomas (1983); rock pools; common.

Dermocarpa violacea form of Entophysalis conferta (Kuetz.) Dr. et D.

Shallow sublittoral; on glass; uncommon.

Entophysalis deusta (Menegh.) Dr. et D.

Sublittoral; endozoic in dead shells and sand-dollars (*Echinarachnius parma*); common.

Schizothrix calcicola (Agardh) Gom. et Gom.

Sublittoral; common as a red film on *Boltenia*.

Spirulina subsalsa Oerst. ex Gom.

Shallow sublittoral; epilithic and on bottles; epizoic on bryozoa; uncommon.

XANTHOPHYCEAE

Vaucheria sp. (a)

Shallow sublittoral; in tufts on sandy bottom in sheltered conditions; rare but locally common.

Vaucheria sp. (b)

Upper littoral; mat-forming in saltmarshes.

OBSERVATIONS AND DISCUSSION

ALGAL ASSEMBLAGES

Estuaries

Five main habitats were recognised between high- and low-tide mark: (i) At mainly upper shore levels, rocky substrata (e.g. embankments) bore fucoids and a species-poor underflora of small green, brown, and red algae. (ii) At middle shore levels saltmarsh, in contrast to solid subtrata, was dominated by mats of green algae (*Blidingia marginata*, *Cladophora sericea*, *Enteromorpha prolifera*, *E. torta*, *Percursaria percursa*, *Rhizoclonium riparium*) and *Vaucheria* spp. Heavy immobile stones bore the *scorpioides* form of *Ascophyllum nodosum*. (iii) At low-shore levels mussel beds in shallow standing water were locally extensively colonised by *Chondrus crispus* and mats of *Chaetomorpha linum*. (iv) Deep pools at low shore levels often contained firm substrata (stones and shells) supporting an assemblage comprising *Chaetomorpha melagonium*, *Chondrus crispus*, *Dumontia contorta*, *Hildenbrandia rubra*, *Petalonia fascia*, *Ralfsia* spp. and *Ulva lactuca*. Shells were often tinged green by shell-boring species such as *Eugomontia sacculata* and *Gomontia polyrhiza*. (v) The lowermost main river channel contained extensive beds of *Zostera marina* (epiphyte free).

Brackish pools

Four main habitats were recognised: (i) Margins colonised by saltmarsh vegetation similar to that in estuaries. (ii) Stones and shells in shallow water that bore occasional fucoids, *Chondrus crispus*, *Hildenbrandia rubra*, *Ralfsia verrucosa* and bleached, delicate tufts of *Polysiphonia fibrillosa*. As in estuaries, shells were often tinged green by shell-boring species. (iii) The soft, silty pool-floors which were extensively blanketed by pale brown mats of *Ectocarpus siliculosus* with occasional *Enteromorpha flexuosa* ssp. *paradoxa* and *E. prolifera*. (iv) *Zostera marina* leaves which were often extensively colonised by epiphytes such as *Erythrotrichia carnea* and *Pilayella littoralis*.

The algal assemblages of the Waweig Estuary and Sam Orr's Pond were similar to some of those found by McLachlan and Edelstein (1971) in the much larger, deeper Bras D'Or Lake in Nova Scotia. We found neither their warm-water assemblages nor the detached ecads of *Ahnfeltia plicata* and *Gracilaria tikvahiae*.

Rocky shores

Littoral assemblages

Most shores (except sites 3 and 10, Indian Point and Point Lepreau) were steeply sloping; the two gently sloping shores examined comprised a series of parallel ridges separated by gulleys. The most obvious feature of all rocky shores was the dense blanketing growths of *Ascophyllum nodosum*. Rocks and pools at high tide level supported patchy *Fucus spiralis* and *Fucus distichus* respectively. Pools in the *Ascophyllum* zone were generally rich in species (*Chondrus crispus*, *Chordaria flagelliformis*, *Corallina officinalis*, *Dumontia contorta*, *Enteromorpha* spp., *Petalonia fascia*, *Rhodomela confervoides*, *Spongomorpha arcta*, *Ulva lactuca* and *Ulvaria obscura* v. *blyttii*). Shaded overhangs and clefts were colonised by *Plumaria elegans* together with its epiphyte *Isthmoplea sphaerophora*.

Fucus evanescens formed a narrow but distinct band at lower shore levels; this alga was sometimes replaced by dense *Mastocarpus stellatus* and *Palmaria palmata*. Lower littoral levels were generally richer in species than upper littoral levels, where blanketing by dense *Ascophyllum* appeared to reduce diversity, and sublittoral levels where grazing by sea-urchins reduced diversity.

Pools at lower littoral or sublittoral fringe levels often contained a well-developed vegetation of predominantly sublittoral species such as *Agarum cribrosum*, *Laminaria saccharina* and *Saccorhiza*

dermatodea. The underflora was often species-rich, containing *Chaetomorpha melagonium*, *Corallina officinalis*, *Devaleraea ramentacea*, *Membranoptera alata*, *Phycodrys rubens*, *Phyllophora pseudoceranoides*, *P. traillii*, *Polysiphonia harveyi*, *Ralfsia fungiformis*, *Scytosiphon lomentaria* and *Spongomorpha spinescens*. Lower shore pools at Point Lepreau (site 10) were particularly rich in Phyllophoraceae (*Ahnfeltia plicata*, *Phyllophora pseudoceranoides*, *P.truncata*). The few wave-exposed rocky shores examined were animal-dominated (barnacles and mussels); at sublittoral fringe levels, *Alaria esculenta* was the most obvious alga.

The sea-shores in the Passamaquoddy area, unlike those in northern New Brunswick and on Prince Edward Island (Gulf of St. Lawrence) are not affected by ice-scour and as a consequence are highly productive in fucoids (particularly *Ascophyllum nodosum*). Stephenson and Stephenson (1954) recorded similar *Ascophyllum*-dominated shores in sheltered locations in Nova Scotia. The north shore of Prince Edward Island, by contrast, bore neither *Ascophyllum* nor the usual associated species (*Fucus spiralis*, *F. edentatus*, *Devaleraea ramentacea* and *Mastocarpus stellatus*); there, the normal littoral dominants *Fucus vesiculosus* and *Chondrus crispus* occurred sublittorally (Bird et al. 1983).

Sublittoral assemblages

A generally consistent pattern of algal occurrence and zonation was detected; it was modified locally by sea-urchin grazing, substratum availability and estuarine effects. For a phytosociological appraisal of the sublittoral algal assemblages of the Passamaquody area and eastern Canada generally, see Tittley et al. (in press, 1988).

At shallow sublittoral fringe levels (+1m to −3m below Chart Datum), the main assemblage was dominated by *Laminaria digitata*; other common constituents were *Agarum cribrosum*, *Desmarestia viridis* and *Saccorhiza dermatodea*. In wave-exposed situations *Alaria esculenta* predominated, contrasting with sheltered shores where *Laminaria saccharina* was predominant. There the *Laminaria* plants were up to 3m in length with delicate blades. They were usually unattached or growing on small stones, often entangled together. The main underflora components beneath *L. digitata* included *Petalonia fascia*, *Polysiphonia urceolata*, *Porphyra miniata* and *Ulvaria obscura*; *Derbesia marina* occurred on sponges at greater depths. Larger species often bore epiphytes (*Ectocarpus fasciculatus* and *Pogotrichum filiformis* were the most obvious). The most common kelp at greater depths was *Agarum cribrosum*; crus-

tose corallines were an obvious, but not dominant, component of the understory vegetation.

At medium depths (−3m to −9m) upright red algae predominated; the most obvious (but occurring only sporadically) brown alga was *Agarum cribrosum*. The dominant species were the slow-growing, urchin-resistant perennials *Phycodrys rubens* (most commonly) and *Ptilota serrata*. Associated species of this assemblage included *Callophyllis cristata*, *Polysiphonia urceolata*, *Scagelia pylaisei*, *Turnerella pennyi* and *Derbesia marina* on sponges. This assemblage was best developed in crevices inaccessible to the green sea-urchin (*Strongylocentrotus droebachiensis*). Many areas were heavily urchin grazed, resembling "urchin-barren-grounds" *sensu* Himmelman (1986) and others. Limpets (*Acmaea testudinalis*) also grazed level boulder tops in the shallow sublittoral. Such situations are characterised by extensive growths of crustose Corallinaceae over rocks and boulders.

In estuaries (fully saline but highly turbid) fewer species were found; the main components of the vegetation beneath *Laminaria longicruris* and *L. saccharina* (if present) were *Polysiphonia urceolata* and the crustose species, *Lithothamnion glaciale*, *Hildenbrandia crouanii* and *Clathromorphum circumscriptum*.

At greater depths (>−10m), animals predominated and provided the main substratum for algal attachment. Surfaces of the sea-potato (*Boltenia*), inaccessible to sea-urchins, were commonly colonised by *Callophyllis cristata* and *Scagelia pylaisei*; also, the surface was frequently covered by a red film of blue-green algae (mainly *Schizothrix calcicola*). Small hydroids bore *Audouinella membranacea* and *A. spetsbergensis*. The most common alga was *Phycodrys rubens*, although *Ptilota serrata* and *Turnerella pennyi* were locally abundant. *Derbesia marina* was widespread as an epiphyte on sponges. In the absence of upright species, crustose Corallinaceae covered shells, stones, cobbles, boulders and bedrock. *Lithothamnion glaciale* and *L. lemoineae* often formed "rhodoliths" and "urchin-barren-grounds" were common. In deeper waters species composition changed, with *Leptophytum laeve* and fleshy crustose red algae (*Peyssonnelia rosenvingii* and the *Cruoria arctica*-phase of *Turnerella pennyi*) becoming locally dominant. Logan et al. (1983) called this species assemblage the "crustose coralline algae Community". Deeper benthic communities (>−18m) below the photic zone were characterized by the common benthic brachiopod *Terebratulina septentrionalis*.

At a few locations in Passamaquoddy Bay and the St. Croix Estuary (Sites 23–29), the deep-water algal communities were absent.

SPECIES OCCURRENCE

Table II shows the paucity of species in the eastern Canadian marine algal flora. Eastern Canada contains only 31% of the total North Atlantic species. The Bay of Fundy (Table II, Columns 5 and 6) is poorer in species (only 69% of the eastern Canadian flora; 21% of the North Atlantic flora), the Passamaquoddy region being poorest (49% of the eastern Canadian flora; 15% of the North Atlantic flora). By comparison, Mathieson and Hehre (1986) recorded 216 taxa in their comprehensive survey of New Hampshire seaweeds. The richer flora can be attributed to more elevated temperatures and a lower incidence of sea urchin grazing; warm temperate or mixed floras in estuarine habitats also enhance the flora.

A comparable survey of Campobello Island (Stone et al., 1970) yielded only 33% of the total eastern Canadian species, while Newfoundland (South and Hooper, 1980) yielded 63%. The flora of Passamaquoddy area, like that of Campobello Island, comprises boreal and subarctic species. The species ratio of Rhodophyceae +

Table 2. Comparative occurrence of species of benthic algae in various North Atlantic locations and in southwestern New Brunswick, Canada.

	Location					
				Bay of Fundy		
	N. Atl.[1]	E. Can.[2]	Nfld.[3]	Passm.[4]	Addtl.[5]	Campo.[6]
R+ C/P*	2.44	1.70	1.88	2.0	–	
Chlorophyceae	253	90	62	45	15	32
Phaeophyceae	324	128	76	58	27	39
Rhodophyceae	539	128	81	68	31	42
TOTAL	1116	346	219	171	73	113

*For R+ C/P, *see* Cheney (1977); (= ratio of Rhodophyceae +Chlorophyceae/Phaeophyceae)

1. South and Tittley (1986)
2. South (1984)
3. South and Hooper (1980)
4. Present survey (excluding species recorded by other authors)
5. Wilson et al. (1979)
6. Stone et al. (1970)

Chlorophyceae Phaeophyceae (R+ C/ P) (Cheney, 1977) for Passamaquoddy Bay is 2.0. This value is typical for cold-temperate/ arctic floras.

Species paucity both in the Passamaquoddy region and in eastern Canada generally can be attributed to the influence of the cold Labrador Current: in the Passamaquoddy area this current holds summer sea temperatures to 8°C (offshore) and 11°C (inshore). Stone et al. (1970) suggested that the poor flora of Campobello Island was also due to its relatively sheltered position at the mouth of the Bay of Fundy. Local factors such as dense *Ascophyllum* cover with little underflora and a heavily grazed sublittoral flora contribute to the species paucity.

New and Interesting Species

Of the 171 species recorded from the Passamaquoddy area, five were new to eastern Canada; a further nine were identified for the first time in the Bay of Fundy. Another sixteen species were found in the Passamaquoddy area for the first time.

Of the Rhodophyceae new to eastern Canada, *Callocolax neglectus* occurred as a parasite on the fronds of *Callophyllis cristata*. It forms irregularly lobed outgrowths or pustules, pale in color (full description in Irvine, 1983). It was first found on European coasts and is widespread there (northern Spain to Norway). The species has also been detected in Newfoundland (R. Hooper, pers. comm.), and New Hampshire (Mathieson and Hehre, 1986). *Hildenbrandia crouanii* is very similar to the common and widespread *H. rubra*; it differs only in having regularly zonate tetraspores (these are obliquely or irregularly divided in *H. rubra* (*see* Newton, 1931). *Phyllophora crispa* consists of a small discoid holdfast and erect fronds with short terete stipes (to 10 mm long), parallel sided blades (100 150) mm long, 10mm broad) and rounded apices. Plants are cartilaginous and bright red to pink (full description in Dixon and Irvine, 1977). Plants collected in the Passamaquoddy area were only 20 30mm long (or smaller), and the fronds divided only once. *Phyllophora crispa* is widespread on European coasts from Norway to Portugal. *Porphyra purpurea* differs from *P. umbilicalis* in the basal (non-central) position of its holdfast; it is distinguished with some diffficulty when plants are torn and tattered.

Sphacelaria caespitula is a small, tufted, filamentous brown alga forming dark-brown confluent mats, as underflora at middle to low shore levels. The filaments are sparingly branched and arise from a distinct basal disc (description in Prud'homme van Reine, 1982).

The *Halicystis ovalis* gametophyte phase of *Derbesia marina* was discovered for the first time in eastern Canada; these pea-like plants (up to 8mm diameter) grew sublittorally on crustose corallinaceae. The only previous northeastern North American record of *in situ H. ovalis* is from New Hampshire (Mathieson and Burns, 1970). South and Tittley (1986) list *D. marina* as widespread in northeastern North America.

Most of the nine species recorded new to the Bay of Fundy were small epiphytes. The *Erythrocystis discigera* form of *Erythrotrichopeltis ciliaris* comprises microscopic confluent monostromatic discs. *Giffordia ovata* is distinguished from other species of the genus by its paired elongate plurilocular sporangia and by the absence of secund branching and corticating filaments; it is uncommon on the coast of eastern Canada. *Mikrosyphar zosterae* differs little from other species of the genus, being distinguished only by its host plant. *Cladophora liniformis*, forming loose-lying mats on littoral sand and mud in saltmarsh among phanerogams (cf. Hoek, 1982) is more common to the south in the United States (South and Tittley, 1986). The discovery of *Rosenvingiella polyrhiza*, an unbranched filamentous plant with distinct lateral rhizoidal outgrowths, occurring in bird roosts in the littoral fringe, represents the southernmost find in northeastern North America (cf. South and Tittley, 1986). *Uronema curvata*, a microscopic, uniseriate filamentous plant epiphytic on the "*Cruoria arctica*" phase of *Turnerella pennyi* in deep water, is a rarity in northeastern North America (South and Tittley, 1986). Of the species not previously recorded from the Passamaquoddy region, most have been found on the Nova Scotia coast of the Bay of Fundy.

Of the 73 species recorded elsewhere in the Bay of Fundy and not found by us (Table l, column 5), many were local rarities; 19 species were largely restricted to the southwestern Nova Scotia (Wilson et al., 1979). Like Stone et al. (1970), we also failed to find *Fimbrifolium dichotomum* and *Polysiphonia nigrescens*, species common elsewhere in eastern Canada. We cannot account for the absence of *Chorda filum*. A few common species were missed by us, probably due to their ephemeral occurrence (e.g. *Monostroma ? pulchrum*, recorded previously in early summer; *Cladosiphon zosterae*, late summer; *Antithamnion cruciatum*, late spring).

ACKNOWLEDGMENTS

This work was supported by N.S.E.R.C. grant A2204 to G. R.

South, and by the British Museum (Natural History). We are grateful to Sandra C. Lindstrom who made unpublished records of southern New Brunswick algae available to us, to Carolyn J. Bird, Christine Maggs, David Garbary and Dean Guthrie, who assisted in the field collections, and Ellen Tracy who assisted in the field and manuscript preparation. Bob Hooper, Memorial University of Newfoundland, confirmed identifications of crustose coralline algae, and Fred Purton of the Huntsman Marine Science Centre assisted with all diving collections. We thank W. McMullon, Department of Fisheries & Oceans Biological Station, St. Andrews, for the preparation of Figure 1.

LITERATURE CITED

Bell, H. P. 1927. Observations of the seasonal disappearance of certain algae in the tide pools near the Biological Station at St. Andrews, N.B. Trans. Nova Scotia Inst. Sci. 17: 1–5.

——— and C. MacFarlane. 1933. The marine algae of the Maritime Provinces of Canada. I. List of species with their distribution and prevalence. Canad. J. Res. 9: 265–297.

Bird, C. J., M. Greenwell and J. McLachlan. 1983. Benthic marine algal flora of the north shore of Prince Edward Island (Gulf of St. Lawrence), Canad. Aquatic Bot. 16: 315–335.

Blair, S. M. 1983. Taxonomic treatment of the *Chaetomorpha* and *Rhizoclonium* species (Cladophorales, Chlorophyta) in New England. Rhodora 85: 175–211.

Cardinal, A. 1968. Repertoire des algues marine benthiques de l'est du Canada. Cah. inf. 48. Québec Min. Industrie Commerce. Stat. Biol. Marine Grande-Rivière.

Cheney, D. P. 1977. R+ C/P — A new and improved ratio for comparing seaweed floras. Abstr., J. Phycol. 13 (suppl.): 12

Colinvaux, L. Hillis. 1959. Marine algae present at St. Andrews, Mascabin Point and Lepreau Ledges, N.B. Tables I, V and VI in: IXth International Botanical Congress, Field Trip 24 (Maritimes).

———. 1966a. Distribution of marine algae in the Bay of Fundy, New Brunswick, Canada. Proc. 5th. International Seaweed Symp. Halifax. 1965: 91–98.

———. 1966b. Herbarium collections of algae from eastern Canada. Taxon 15: 166.

Dixon, P. S. and L. M. Irvine. 1977. Seaweeds of the British Isles Volume I Rhodophyta part 1. Introduction, Nemaliales, Gigartinales. British Museum (Natural History). London.

Edelstein, T., L. Chen and J. McLachlan. 1970. Investigations of the marine algae of Nova Scotia. VIII. The flora of Digby Neck Peninsula, Bay of Fundy. Canad. J. Bot. 48: 621–629.

Fowler, J. 1901. A visit to St. Andrews, N.B., with a catalogue of plants collected in its vicinity. Proc. Nova Scotia Nat. Hist. Ass. Miramichi 1: 21–28.

———. 1902. Report on the flora of St. Andrews, N.B. Contr. Canad. Biol. 1902 1905: 41–48.

HAY, G. U. 1886. Marine algae of the Bay of Fundy. Bull. Nat. Hist. Soc. New Brunswick 1: 32–33.

_____. 1887a. Marine algae of the Maritime Provinces (with "Introductory list of the marine algae of the Maritime Provinces, with notes" by G. U. Hay and A. H. MacKay). Bull. Nat. Hist. Soc. New Brunswick 1: 62–68.

_____. 1887b. Marine algae of New Brunswick (with an appendix containing a list of the marine algae of the Maritime Provinces of the Dominion of Canada, with notes by G. U. Hay and A. H. MacKay). Proc. and Trans. Roy. Soc. Canada, 1887, Sec. IV, 5: 167–174.

HEHRE, E. J., J. R. CONWAY AND R. A. STONE. 1970. Flora of the Wolf Islands. Part III: The marine algae. Rhodora, 72: 115–118

HIMMELMAN, J. H. 1986. Population biology of green sea urchins on rocky barrens. Mar. Ecol. Progr. Ser. 33: 207–216.

HOEK, C. VAN DEN. 1982. A Taxonomic Revision of the American Species of *Cladophora* (Chlorophyceae) in the North Atlantic Ocean and Their Geographic Distribution. North-Holland Publishing Co., Amsterdam.

IRVINE, L. M. 1983. Seaweeds of the British Isles Vol. 1. Rhodophyta Part 2A Cryptonemiales (sensu stricto). Palmariales, Rhodymeniales. British Museum (Natural History), London.

KLUGH, A. B. 1916. The marine algae of the Passamaquoddy region, New Brunswick. Contr. Canad. Biol. Suppl. to 5th Ann. Report: 79–84.

_____. 1924. Factors controlling the biota of tide pools. Ecology 5: 192–196.

LINKLETTER, L. E., E. I. LORD AND M. J. DADSWELL. 1977. A Checklist and Catalogue of the Marine Fauna and Flora of the Lower Bay of Fundy Shore of New Brunswick. Huntsman Marine Laboratory, St. Andrews, N.B.

LOGAN, A., A. A. MACKAY AND J. P. A. NOBLE. 1983. Sublittoral hard substrates. *In:* M. Thomas, Ed. Marine and coastal systems of the Quoddy Region, New Brunswick. Canad. Spec. Publ. Fish. Aquat. Sci. 64.

MACFARLANE, C. I. AND G. M. MILLIGAN. 1965. Marine Algae of the Maritime Provinces of Canada, a Preliminary Checklist. Nova Scotia Research Foundation, Halifax.

MACKAY, A. A. 1978. Bay of Fundy Investigation. St. Croix River Passamaquoddy Bay. Marine Research Associates Ltd., Report to N.B. Dept. of Fisheries.

MCLACHLAN, J. AND T. EDELSTEIN. 1971. Investigations of the marine algae of Nova Scotia. IX. A preliminary survey of the flora of Bras D'Or Lake, Cape Breton Island. Proc. Nova Scotia Inst. Sci.27: 11–22.

MATHIESON, A. C. AND R. L. BURNS. 1970. The discovery of *Halicystis ovalis* (Lyngbye) Areschoug in New England. J. Phycol. 6: 404–405

_____ AND J. M. HEHRE. 1986. A synopsis of New Hampshire seaweeds. Rhodora 88: 1–139

NEWTON, L. 1931. A Handbook of the British Seaweeds. British Museum (Natural History), London.

NIELSEN, R. AND J. MCLACHLAN. 1986. Investigations of the marine algae of Nova Scotia. XVI. The occurrence of small green algae. Canad. J. Bot. 64: 808–814.

PRUD'HOMME VAN REINE, W. F. 1982. A Taxonomic Revision of the European Sphacelariaceae. E. J. Brill, Leiden.

SMITH, D., K. LYNCH, J. FRANKS, E. FRASER, H. PAINTER, D. SAUNDERS, A. WALKER AND S. WILSON. 1978. Investigations of the ecology of the Bay of Fundy. Productivity and nitrogen flow in a Minas Basin saltmarsh, and distribution of macro-algae in the Bay of Fundy (New Brunswick shore). Project 16-01-001 N.R.C. Atlantic Regional Laboratory, Halifax.

SOUTH, G. R. 1976. A check-list of marine algae of eastern Canada — first revision. J. Mar. Biol. Assoc. U.K. 56: 817 843.

———. 1984. A checklist of marine algae of eastern Canada. 2nd Rev. Canad. J. Bot. 62: 680 704.

——— AND A. CARDINAL. 1970. A checklist of marine algae of eastern Canada. Canad. J. Bot. 48: 2077-2095.

——— AND R. G. HOOPER. 1980. A catalogue and atlas of the benthic marine algae of the island of Newfoundland. Occas. Pap. Biol. Mem. Univ. Nfld. 3: 1-136.

——— AND I. TITTLEY. 1986. A checklist and distributional index of the benthic marine algae of the North Atlantic Ocean. Huntsman Marine Laboratory and British Museum (Natural History), St. Andrews and London.

STEPHENSON, T. A. AND A. STEPHENSON. 1954. Life between tide-marks in North America. IIIA. Nova Scotia and Prince Edward Island: description of the region. J. Ecol., 42: 14-45.

STONE, R. A., E. J. HEHRE, J. M. CONWAY AND A. C. MATHIESON. 1970. A preliminary checklist of the marine algae of Campobello Island, N. B., Canada. Rhodora 72: 313 338.

TAYLOR, W. R. 1957. Marine Algae of the Northeastern Coast of North America. Univ. Michigan Press, Ann Arbor.

THOMAS, M. L. H. ED. 1983. Marine and coastal systems of the Quoddy Region, New Brunswick. Canad. Spec. Publ. Fish. Aquatic Sci. 64, Dept. Fish. & Oceans, Ottawa.

TITTLEY, I., W. F. FARNHAM, R. G. HOOPER AND G. R. SOUTH. 1988. Sublittoral seaweed assemblages (2): a transatlantic comparison. Progr. Underwater Sci. 13: (in press).

WILSON, J. S., C. J. BIRD, J. MCLACHLAN AND A. R. A. TAYLOR. 1979. An annotated checklist and distribution of benthic marine algae of the Bay of Fundy. Occas. Pap. Biol. Mem. Univ. Nfld. 2: 1 65.

G. R. S.
HUNTSMAN MARINE SCIENCE CENTRE
ST. ANDREWS, NEW BRUNSWICK, CANADA, E0G 2X0

I.T.
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD, LONDON, SW7 5BD
UNITED KINGDOM

W. F. F.
PORTSMOUTH POLYTECHNIC, MARINE LABORATORY
FERRY ROAD, HAYLING ISLAND, PO11 0DG
UNITED KINGDOM

D. W. K.
DEPARTMENT OF BIOLOGY AND NEWFOUNDLAND
INSTITUTE FOR COLD OCEAN SCIENCE
MEMORIAL UNIVERSITY OF NEWFOUNDLAND
ST. JOHN'S, NEWFOUNDLAND
CANADA, A1B 3X9

RHODORA, Vol. 90, No. 864, 1988

NEW ENGLAND NOTE

POLEMONIUM VANBRUNTIAE (POLEMONIACEAE) IN MAINE

DAVID M. JOHNSON AND NANCY A. MURRAY

In the course of botanical exploration in and around the Great Heath northeast of Cherryfield, Washington County, Maine, we discovered a population of about a dozen stems, perhaps representing only a single clone, of *Polemonium vanbruntiae* Britton (Polemoniaceae). This uncommon and local species, endemic to the northeastern United States, was previously known from scattered localities in West Virginia, Maryland, Pennsylvania, New Jersey, New York, and Vermont. This new locality represents the first occurence of the species in Maine, and a range extension of about 375 km northeastward from the Vermont stations. The plant was in full flower on 5 July 1987, growing in a shaded area with mucky soil on the border of the Great Heath with species of *Carex*, *Dryopteris*, and *Osmunda*. The site, less than 100 m in elevation, is in the SW 1/4 of Township 18 MD BPP ca. 3/4 mile north of Schoodic Lake in southern Washington County. A voucher specimen, *Johnson & Murray 1652*, has been deposited at NY.

Polemonium vanbruntiae was reported for Maine by Ogden et al. (1948), who listed it for Knox County. Fernald (1949) stated shortly thereafter that the specimen of *Polemonium* collected at Matinicus, Knox County, in 1919 (*C. A. E. Long s.n.*, NEBC) was the European *P. caeruleum* L., escaping in an old cemetery; our examination of this specimen sent on loan confirmed Fernald's determination. *Polemonium vanbruntiae* was thus undocumented from Maine until the present time.

The two species are, however, closely related. Davidson (1950), in a monograph of *Polemonium*, reduced *P. vanbruntiae* to a subspecies of *P. caeruleum*, the nominate subspecies being restricted to Eurasia. Floristic manuals for the region, however, continue to recognize the two taxa as distinct species (Fernald, 1950; Gleason and Cronquist, 1963; Seymour, 1969, 1982), emphasizing the consistent differences between the two in stamen exsertion, number of leaflets, and rhizome habit.

A second species of *Polemonium*, *P. cuspidatum* Sieb. & Zucc., is listed for Aroostook County, Maine, by Richards et al. (1983). We have been unable to trace this name in any index or in the literature, and have concluded that the name *Polygonum cuspidatum* Sieb. & Zucc. was somehow misplaced under *Polemonium* (*Polygonum cuspidatum* was reported from Aroostook County in this same checklist).

Polemonium vanbruntiae should be sought in other shaded boggy habitats in Maine; it is extremely local throughout its range, and efforts should be made for its protection and study.

ACKNOWLEDGMENTS

We thank Ingrid and Joerg H. Lotze of Eagle Hill Wildlife Research Station, Steuben, Maine, for making it possible for us to do field work in Maine during the summer of 1987. The assistance of Allan Bornstein, Allison Dibble, Sally Rooney, Moody F. Trevett, two anonymous reviewers and the curators of the NEBC herbarium is gratefully acknowledged.

LITERATURE CITED

DAVIDSON, J. F. 1950. The genus *Polemonium* (Tournefort) L. Univ. Calif. Publ. Bot. 23: 209–282.

FERNALD, M. L. 1949. An abbreviated flora of Maine (Review). Rhodora 51: 5–8.

———. 1950. Gray's Manual of Botany, 8th ed. D. Van Nostrand Company. New York.

GLEASON, H. A., AND A. CRONQUIST. 1963. Manual of Vascular Plants of the Northeastern United States and Adjacent Canada. D. Van Nostrand Company. New York.

OGDEN, E. C., F. H. STEINMETZ, AND F. HYLAND. 1948. Check-list of the vascular plants of Maine. Bull. Josselyn Bot. Soc. Maine 8: 1–70.

RICHARDS, C. D., F. HYLAND, AND L. M. EASTMAN. 1983. Revised check-list of the vascular plants of Maine. Bull. Josselyn Bot. Soc. Maine 11: 1–73.

SEYMOUR, F. C. 1969. The Flora of New England. Charles E. Tuttle Company. Rutland, Vermont.

———. 1982. The Flora of New England, 2nd ed. Phytologia Memoirs 5: 1–611.

NEW YORK BOTANICAL GARDEN
BRONX, NY 10458

RHODORA, Vol. 90, No. 864, 1988

NEW ENGLAND NOTE

TWO NEW STATIONS FOR *DRYOPTERIS FRAGRANS* IN VERMONT

ARTHUR V. GILMAN

Dryopteris fragrans (L.) Schott, fragrant wood fern, was considered frequent throughout its range (occurring in 50% of possible sites of proper habitat) by Lellinger (1985). In eastern North America it reaches the southern limit of its range in Vermont, where its occurrence is much less common. Zika and Dann (1985) proposed 'rare' status for it in Vermont as it has historically been known from fewer than ten locations within the state.

In Vermont, *Dryopteris fragrans* is epipetric on shaded schist or granite outcrops of boreal character, usually at high elevation and northern or eastern aspect. Often it occurs under overhangs, which provide shade. No Vermont stations have heretofore been recorded east of the Green Mountains, despite the existence of suitable habitat, especially in the northeast highlands.

Two new stations have recently been discovered in Groton State Forest in Peacham, Vermont, on Owl's Head and Big Deer Mountain. A population of approximately 40 individuals occurs near the base of south-facing granite cliffs at Owl's Head, at an elevation of 1800 ft. One or two of the largest plants grow in full sun, but the majority are well shaded by overhangs. The extent of this particular habitat is not great, and *Dryopteris fragrans* is the dominant element. A second and larger population of approximately 200 individuals occurs two miles east on Big Deer Mountain, part of the same granite formation. Here, although the elevation is not much higher (approximately 1900 ft.), the aspect is eastern and the site is shaded by trees. The fern grows in soil along the base of the ledges as well as in overhangs and crevices in the face of the ledge. At both locations, many of the individuals have laminae reaching 25 cm in length, easily qualifying them as *D. fragrans* var. *remotiuscula* Komarov.

Soil samples taken from the root zone of the plants at Big Deer Mountain have an average pH of 4.15, and the granite has a pH of 3.9. Although *D. fragrans* is occasionally mentioned in the literature

as preferring calcareous substrates, it appears to be indifferent to soil reaction even at the limit of its distribution.

Other ferns occurring on these cliffs, at both locations, are *Polypodium virginianum* L., *Cystopteris fragilis* (L.) Bernh., and *Dennstaedtia punctilobula* (Michx.) Moore. *Dryopteris marginalis* (L.) A. Gray appears in talus below the ledges, but a search for the possible hybrid *D.* × *algonquinensis* Britton (*D. fragrans* × *marginalis*) has proved fruitless. Other ferns of northern distribution such as *Woodsia glabella* R. Brown and *Asplenium viride* Huds., or calcophilic ferns such as *Pellaea glabella* Mett. ex Kuhn have not been found at either site.

LITERATURE CITED

LELLINGER, D. B. 1985. A Field Manual of the Ferns and Fern Allies of the United States and Canada. Smithsonian Institution Press. Washington, D.C.

ZIKA, P. F. AND K. T. DANN. 1985. Rare plants on ultramafic soils in Vermont. Rhodora 87: 293–304.

BOX 82
MARSHFIELD, VT 05658

APPENDIX

Exsiccatae for *Dryopteris fragrans* (L.) Schott in Vermont

Bennington Co.: Manchester, N side of Cook's Hollow, Mt. Equinox, 2700 ft., *Jenkins & Sorrie 83–92* (VT). Caledonia Co.: Peacham, Owl's Head, 1800 ft., 1986, *A. Gilman s.n.* (VT); Peacham, Big Deer Mt., 1900 ft., 1987, *A. Gilman s.n.* (Herb. A. V. Gilman). Chittenden Co.: Underhill, Nebraska Notch, high cliffs, 1906, *E. Strauss s.n.* (VT). Lamoille Co.: Cambridge, Smuggler's Notch 1893, *A. J. Grout s.n.* (VT); Stowe, under the nose of Mt. Mansfield, 1896, *F. A. Balch s.n.* (VT); E side of Mt. Mansfield, 3700 ft., *Zika 4730* (VT). Rutland Co.: Hubbardton, Mt. Zion, *Eggleston 2467* (VT). Washington Co.: Duxbury, exposed cliff of Camel's Hump, 4000 ft., 1943, *R. H - (?) s.n.* (VT); E side of Camel's Hump, ledges between Alpine Trail and Forestry Trail, 3000 ft., *Zika 77-3-13* (VT). Windsor Co.: Rochester, bare ledges, S exposure, Mt. Horrid, 1920, *D. L. Dutton s.n.* (VT).

RHODORA, Vol. 90, No. 864, 1988

NEW ENGLAND NOTE

GROWTH AND EXTENSION OF A NATURALIZED WESTERN MASSACHUSETTS STAND OF *CATALPA SPECIOSA* WARDER

C. JOHN BURK AND VIKRAM PRABHU

High mortality accompanied by low recruitment of native floodplain tree species was observed in western Massachusetts oxbow forests during the period 1975-1985 (Holland and Burk, 1986). A population census of hardy catalpa, *Catalpa speciosa* Warder, in the vicinity of one of these oxbows was first conducted in 1975 (Burk and Lauermann, 1977); the stand was reinvestigated in 1987 to determine whether this naturalized and recently invasive species has experienced a comparable decline. The population originally extended from a road edge into floodplain forest on the east and west banks of the Mill River in Northampton, Hampshire Co., occurring in association with *Acer saccharinum* L., *Populus deltoides* Marsh., *Fraxinus pennsylvanica* Marsh., and *Ulmus rubra* Muhl. Hardy catalpa apparently became established on this site some time after 1939 when the Mill River was diverted into its present channel; the oldest *C. speciosa* in the stand in 1975 was an estimated 32 years of age.

In late October, 1987, we located all specimens of *Catalpa speciosa* along the road edge and in the floodplain forest. Since 1975, the population has also expanded southeast beyond the forest into an adjacent old field. Diameters of all catalpas encountered were measured at four feet (1.2 m) above ground to establish "diameter breast height" or dbh. Data were grouped in size classes for comparison with those from 1975 (Figure 1). An additional size class beyond those used in 1975 was added to accommodate tree growth.

So far as we could tell, no specimens of *Catalpa speciosa* in the forest had died in the twelve-year interval. Growth increments shifted the distribution of many trees into higher size classes and at least nine saplings were recruited into the lowest class. The three largest trees and a double-trunked tree with main stems 23.2 and 22.0 cm dbh produced capsules in 1987; in contrast, only two trees fruited in 1975. Although no logging or other cutting of *C. speciosa* occurred in the forest, several of the largest trees along the road edge

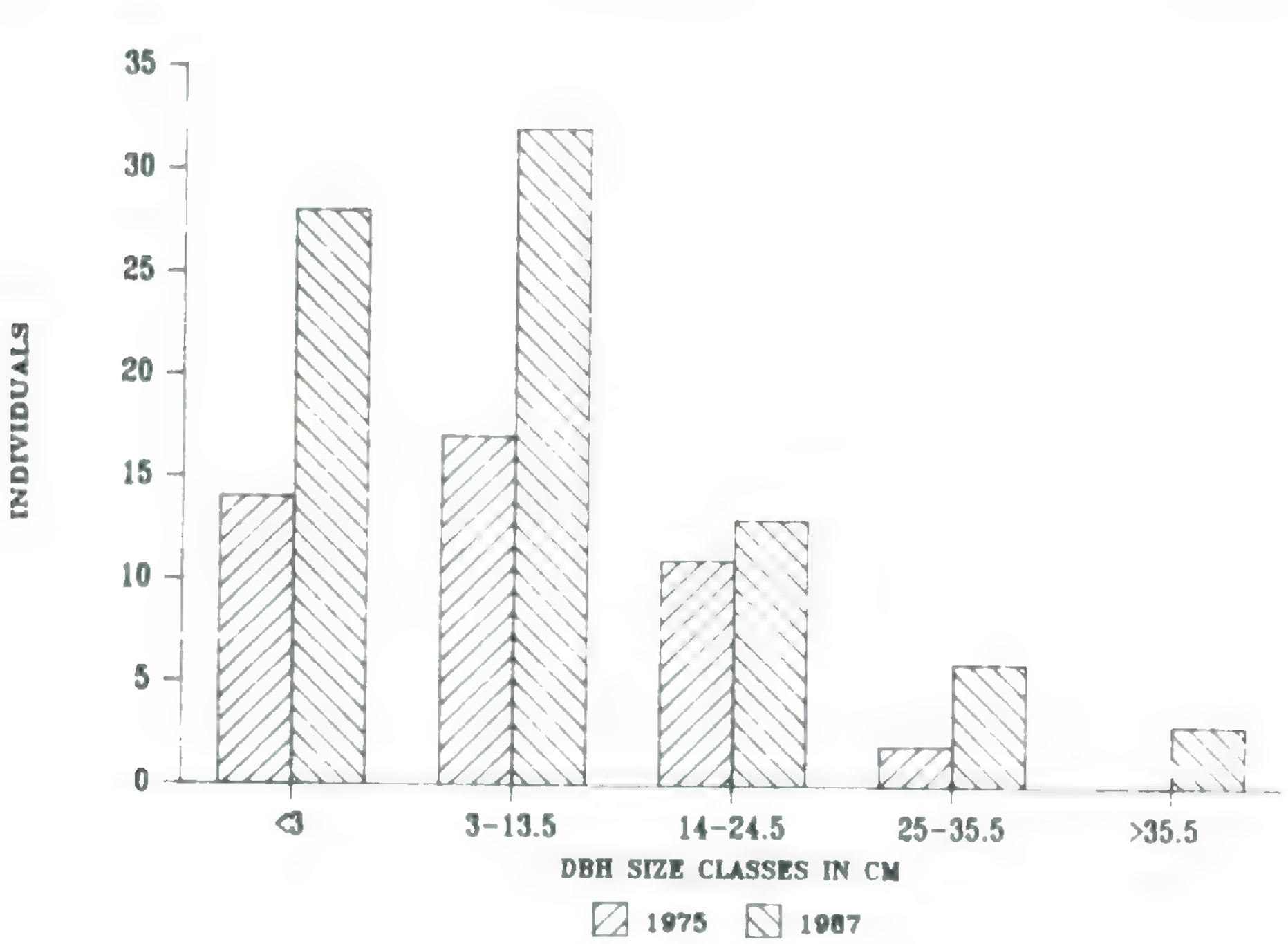


Figure 1. Number of individuals within diameter classes (cm) of *Catalpa speciosa* population, 1975 and 1987, excluding road edge trees.

were cut during or soon after the 1975 field period; these resprouted and showed substantial growth by 1987. All catalpas in the old field population were in the two smaller size classes except for one tree 14.5 cm dbh. A number of the old field catalpas had been cut to the ground at least once.

Throughout the 1975–1987 interval, the floodplain forest, road edge, and adjacent fields were periodically flooded, with a major and lengthy inundation during late May, 1984. In an adjacent oxbow of the Connecticut River, a re-examination of swamp forest quadrats indicated tree deaths and low recruitment over the period 1975–1985 for *Acer saccharinum, Fraxinus pennsylvanica, Populus deltoides, Quercus palustris* Muenchh., and *Salix nigra* Marsh. as well as for several less abundant associates (Holland and Burk, 1986). For all species, mortality was highest in the smallest (3–13.5 cm dbh) size classes, but larger (36–46.5 cm dbh) *Q. palustris* also died.

The continued growth and population expansion of *Catalpa speciosa* during a time of evident stress for native tree species in the vicinity suggests that *C. speciosa* may become an increasingly important component of floodplain forests and old fields in the region.

LITERATURE CITED

BURK, C. J. AND S. D. LAUERMANN. 1977. *Catalpa speciosa* naturalized in western Massachusetts. Rhodora 79: 305–307.

HOLLAND, M. M. AND C. J. BURK. 1986. Tree death and low recruitment in two western Massachusetts floodplain forests. Amer. J. Bot. 73: 668.

DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON, MA 01063

RHODORA, Vol. 90, No. 864, 1988

NEW ENGLAND NOTE

THE SPREAD OF *CATALPA OVATA* G. DON IN WESTERN MASSACHUSETTS AND ITS BIOGEOGRAPHIC IMPLICATIONS

C. JOHN BURK AND NANCY D. MCMASTER

The genus *Catalpa* (Bignoniaceae) has a disjunct occurrence in eastern North America and the West Indies and in eastern Asia (Li, 1971). Three of the eleven modern *Catalpa* species have been collected in New England. *Catalpa bignonioides* Walt., native to southeastern United States, was formerly more widely planted (Blakeslee and Jarvis, 1913) and is rarely adventive in the area. *Catalpa speciosa* Warder is native to the Mississippi River drainage system from southwestern Indiana and southern Illinois south possibly as far as Louisiana (Little, 1979) and may have occurred farther eastward as recently as 1500–1700 A.D. (Hemmings and Core, 1976). In western New England, *C. speciosa* has become increasingly abundant, occurring on various disturbed sites with at least one well-established regenerating population in a relatively undisturbed floodplain forest (Burk and Lauermann, 1977). *Catalpa ovata* G. Don, native to central China (Li, 1971), is escaped and naturalized from Connecticut to southern Ontario, Ohio and Maryland (Fernald, 1950). Seymour (1982) cited specimens of *C. ovata* from Avon and North Branford, CT and from Norwich, VT.

We know of no previous Massachusetts reports of *Catalpa ovata*. However, we have examined two unreported Massachusetts collections of this species, both in MASS by the late H. E. Ahles (*Ahles 77963*, July 22, 1973 from a river bank in Huntington, Hampshire Co. and *Ahles 86013*, July 31, 1978 from a river bank in Holyoke, Hampden Co.) In addition, Bruce Sorrie has called our attention to a third western Massachusetts collection in VT by Peter F. Zika and R. G. Poland (*Zika 6732*, Oct. 3, 1982 from a thicket along the Connecticut River on River Road, Deerfield, Franklin Co.) Label data indicate that *C. ovata* is naturalized in the vicinity of the Deerfield site.

In June, 1987, we observed a stand of *Catalpa ovata* naturalized in several partially overgrown pastures in Shelburne, Franklin Co., MA along a 1 km stretch of Little Mohawk Road in the area known

locally as "the Patten." The trees occur in a southward-facing ravine, extending from an elevation of 1050 ft. (320 m) down to about 850 ft. (259 m) and from the road edge inward for a distance of as much as 100 m. The site is underlain by shallow well-drained loam with frequent rock outcroppings (U. S. Department of Agriculture, 1967). The catalpas grow both scattered and clumped throughout the pastures in association with *Berberis thunbergii* DC., *Juniperus communis* L., *Tsuga canadensis* (L.) Carr. and other invasive woody species. We did not find *C. ovata* in woodlands adjacent to the pastures. The trees had well-formed flower buds on June 19, flowered for three weeks beginning around June 27, and were releasing seeds from their capsules October 2. A census on October 2 estimated the population at approximately 200 specimens; a precise count of individuals was impossible without causing unwarranted disturbance to the stand because of a number of dense clusters of stems which may have been either separate crowded trees or groups of clonal shoots from cut-over stems or layered branches.

The Shelburne *Catalpa ovata* population occurs on property now owned by R. H. Goldthwaite. Mr. Goldthwaite believes all are descended from a single specimen planted a few years after the land was purchased by his family in 1909. This original tree was felled in the 1960's. The largest tree at present occurs on the road edge adjacent to the Goldthwaite house and measures 51 cm in diameter at four feet (1.2 m) from the ground; the age of this tree was determined by increment borings to be approximately 55 years. Mr. Goldthwaite reported that the catalpas spread through wind-blown seeds, through capsules which had been discarded with lawn debris on one pasture and, on the northern edge of the property, as escapes from a few transplanted trees on adjacent propery. He has observed that the catalpas are unpalatable to cattle, become weedy and aggressive in the pasture, regenerate from newly-cut stumps "as much as four or five feet in a single season," and fail to spread into wooded areas.

The inter-relationships of *Catalpa bignonioides, C. speciosa* and *C. ovata* have been of general biosystematic interest. *Catalpa bignonioides* and *C. speciosa* may be confusingly similar, and Seymour (1982) presents useful criteria separating them on the basis of leaf morphology. *Catalpa ovata* is easily distinguished from both *C. bignonioides* and *C. speciosa* by its smaller, predominantly yellow corollas, its shorter narrower capsules, and its glabrous or quickly glabrate leaves (Fernald, 1950; Seymour, 1982). Nonetheless *C. ovata* hybridizes easily with *C. bignonioides* and the hybrids are

fully fertile and vigorous (Smith, 1941). Describing the similarity of the chromosomes of *C. ovata* and *C. bignonioides*, Smith (1941) noted evidence that *C. ovata* and *C. speciosa* are equally interfertile.

If *Catalpa* species continue to spread outside their present disjunct ranges, it seems possible that populations of *C. ovata*, *C. speciosa* and/or *C. bignonioides* will overlap sufficiently for more extensive interbreeding to occur. We know of no naturalized stands of *Catalpa bignonioides* in our area. At present, however, the nearest flowering specimen of *C. speciosa* to *C. ovata* at Shelburne is a large dooryard tree only .75 km distant. In April, 1988, we also observed mature trees of *C. speciosa* in the vicinities of the Huntington and Deerfield sites for *C. ovata*.

We have attempted to contrast the Shelburne population of *Catalpa ovata* with naturalized *C. speciosa* in western Massachusetts (Burk and Lauermann, 1977 and more recent observations). Comparisons suggest that the two species, at least as represented here, possess somewhat different ecological characteristics as well as distinct morphologies. Naturalized *C. ovata* at Shelburne occupies an open, upland site, although both Ahles collections and the Zika and Poland specimen from Deerfield were taken from river banks or their vicinities. *Catalpa speciosa* commonly escapes along stream edges and competes successfully in mature floodplain forests. *Catalpa ovata* at Shelburne flowered from late June through mid-July and the Ahles collections were made while the trees were in flower still later in July; *C. speciosa* blooms earlier and was observed in full flower in lowlands along the Deerfield River in Shelburne on June 18. *Catalpa ovata* at Shelburne flowers and sets fruit at an early age with specimens no taller than 2 m producing capsules in 1987; only the largest and oldest specimens of *C. speciosa* on the flood plain have been observed in fruit or flower.

The current natural range of *Catalpa* represents a contraction of a broad, circumpolar Tertiary distribution (Graham, 1972; Li, 1971). Recognizing this, Stebbins (1950) used *C. ovata* and *C. bignonioides* as examples of morphologically distinct allopatric species which are ecologically equivalent in regions of similar climate; he suggested that if the geographic barrier separating *C. ovata* from *C. bignonioides* were removed, the two would "very likely revert to subspecies of a single species." Grant (1971), citing Stebbins, considered *C. ovata* and *C. bignonioides* at the "semispecies level of divergence." Similar comparisons might be made for *C. ovata* and *C. speciosa*. Thus, existing naturalized *Catalpa* stands should be monitored for

possible interspecific hybridization, especially hybridization between the American and east Asian species, since analyses of any hybrid populations and the degree to which the species maintain their morphological and ecological identities may provide useful insights into processes of speciation both in *Catalpa* and in other similarly disjunct taxa. Specimens of *C. ovata* from the Shelburne population have been deposited in SCHN and MASS. We are grateful to Marian Rohman at MASS and Linda M. Prince at VT for their assistance with this project.

LITERATURE CITED

BLAKESLEE, A. F. AND C. D. JARVIS. 1913. Trees in Winter. MacMillan Co., New York.

BURK, C. J. AND SCOTT D. LAUERMANN. 1977. Catalpa speciosa naturalized in Western Massachusetts. Rhodora 79: 305–307.

FERNALD, M. L. 1950. Gray's Manual of Botany, 8th Ed. American Book Co., New York.

GRAHAM, A., ED. 1972. Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Publishing Co., Amsterdam.

GRANT, V. 1971. Plant Speciation. Columbia U. Press, New York.

HEMMINGS, E. T. AND E. L. CORE. 1976. Archeological evidence for range extension of the Catawba tree (*Catalpa speciosa* Warder) in West Virginia. Castanea 41: 9 11.

LI, H. 1971. Floristic Relationships between Eastern Asia and Eastern North America. The Morris Arboretum, Philadelphia, Pennsylvania.

LITTLE, E. L. 1979. Checklist of United States Trees (Native and Naturalized). Agricultural Handbook No. 541, U.S. Government Printing Office, Washington, D.C.

SEYMOUR, F. C. 1982. The Flora of New England, 2nd ed. Phytologia Memoirs, V. H. N. and A. L. Moldenke Publishers, Plainfield, New Jersey.

SMITH, E. C. 1941. Chromosome behavior in *Catalpa hybrida* Spaeth. J. Arnold Arb. 22: 219 221.

STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia U. Press, New York.

U.S. DEPARTMENT OF AGRICULTURE. 1967. Soil Survey, Franklin County, Massachusetts. Soil Conservation Service, Washington, D.C.

DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON, MA 01063

RHODORA, Vol. 90, No. 864, 1988

BOOK REVIEW

STEPHEN W. EATON AND EDITH FEUERSTEIN SCHROT. *A Flora of the Vascular Plants of Cattaraugus County, New York.* Bulletin of the Buffalo Society of Natural Sciences 31. iv + 235 pp. + 2 foldout maps. 1987. ISBN 0-944032-50-8. (Price: U.S. $15.95, plus $1.25 for shipping and handling.)

Situated near the southwestern corner of New York State immediately north of Pennsylvania, the 3400 km^2 of Cattaraugus County encompass parts of the glaciated and unglaciated Allegheny Plateau, a combination found nowhere else in the state. The distribution of plants in the county somewhat reflects this topographic difference, but the contrast is more apparent in the landforms and in the occurrence of habitats, particularly kettle-hole ponds and other glacial features north of the terminal moraine and rock-cities (local areas of deeply and often broadly fissured residual conglomerate blocks) south of it. The county's habitat diversity has attracted repeated exploration, particularly by botanists from Buffalo and Albany, and the authors, through their own diligent collecting, have added much new information in recent years. They have clearly and usefully summarized what is known of the flora, following the pattern of C. A. Zenkert's distinguished *Flora of the Niagara Frontier Region* (1934), an area defined as within 50 miles of Buffalo.

Eaton's and Schrot's *Flora* consists of an annotated list of species organized systematically, following Cronquist for the angiosperms. For each entry, a common name, habitat notes, details about localities (for infrequent species only), and phenological data (flowering and fruiting times) are provided. There are no keys or other identification aids, although photographs of a few noteworthy species are included. The many photographs of habitats should prove useful as historic records. Numerous significant new distributional records are published, and the location of voucher specimens for these is indicated. For the most part, the names adopted for species reflect contemporary taxonomic and nomenclatural scholarship. They mostly correspond with names in R. S. Mitchell's *A Checklist of New York State Plants* (1986), even though the two publications were in press simultaneously. The 1280 species (923 native, 357

introduced) listed by Eaton and Schrot for Cattaraugus County compare with the 3395 species (1999 native, 1396 non-native) enumerated by Mitchell for all of New York State.

The plant distributional records assembled over the years by the botanical staff of the New York State Museum—mainly maps and specimen and literature citations for each species known from the state, together with county checklists derived from these data—form an indispensable starting point for floristic treatments of small subunits of New York. An examination of a portion of these files (pteridophytes and monocots only) in connection with the preparation of this review revealed records for 10 species that appear not to have been accounted for by Eaton and Schrot. I draw attention to this file because of its uniqueness and the time it will save others compiling catalogs of records of New York plants.

Apart from being an authoritative source of botanical information, this Flora serves also as a naturalist's guide to Cattaraugus County. Many aspects of the physical and biological environment are described succinctly and illustrated with maps and photographs, including climate, soils, bedrock and glacial geology, forest types and their postglacial history, specific habitats and associated flora, the geographic relationships of the flora, and a synopsis of species that have or are in the process of spreading rapidly in the county. These narrative vignettes provide depth and interest.

Stephen Eaton, now retired as a Biology Professor from St. Bonaventure University, is an authority on the natural history of southwestern New York. Much valuable information has resulted from the many years he has had the animals and plants of this and the adjacent region under scrutiny. He has been joined by an able co-worker. Together, they have given us a Flora of lasting value, and one written by authors with much first-hand experience with plants in the field.

NORTON G. MILLER
BIOLOGICAL SURVEY
NEW YORK STATE MUSEUM
THE STATE EDUCATION DEPARTMENT
ALBANY, NY 12230

RHODORA, Vol. 90, No. 864, 1988

BOOK REVIEW

HAROLD R. HINDS. *Flora of New Brunswick.* 460 pp. + xxvi, 1,524 illus., 1,008 distribution maps. Available from the author, Biology Department, University of New Brunswick, Fredericton, N.B., Canada, E3B 6E1. 1986. ISBN 0-9692456-0-2. (Price: $30.00 Canadian).

The 1986 *Flora of New Brunswick* by Harold R. Hinds is an outstanding contribution to floristic botany and a remarkable achievement in regional plant science.

Until the publication of the *Flora,* there existed no inventory of this aspect of the province's living natural resources. There were bits of information scattered in various lists and in old records, or on herbarium sheets, but none of this was systematic, complete, or up-to-date, nor was it available to plant scientists, resource managers, and others. Prior to the publication of this flora, botanists had to turn to the broader-ranging, *Gray's Manual,* or to the narrower-ranging floras of adjacent provinces. These works permitted the identification of many of New Brunswick's plants, but they gave no indication of a species' status in the province.

Now, with the *Flora of New Brunswick,* complete with its keys to families, genera and species, with both French and English common names, and with its illustrations, habitat descriptions, and distribution maps, the serious study of the vascular plants of New Brunswick can begin.

The flora is clearly printed on good quality paper, stitch bound in fascicles. With relatively little persuasion, the book lies open at the pages to which it is turned. The book's soft cover, decorated with an attractive drawing of the region's rare endemic, *Pedicularis furbishiae* Wats., is plasticized on the outside. Some few typographical errors can certainly be corrected in succeeding editions.

Bracketed dicotomous keys, beginning with a key to families, are used throughout the work. From the key to families, the user is led to other parts of the book where keys to genera and species are found distributed under their families. The keys can readily be traced backwards because each couplet is preceded by the number and letter, in parenthesis, of the previous couplet the user has followed. Thus, anyone using the key can easily backtrack to make an alternate choice, or to construct a concise description of a taxon.

The species are arranged alphabetically within each genus, and the genera alphabetically within families, which in turn are arranged according to the familiar sequence of Engler and Prantl. Under each species, the author has recorded recent synonyms, and, where such exist, the French and English common names. Included also are notes on the habitat, distribution and frequency of the species in New Brunswick and a note on the species' general range in North America. Subspecific taxa, when present in the province, are also noted.

The nomenclature is, perhaps, the most up-to-date of any North American flora, while still being somewhat conservative. The name *Reynoutria japonica* Houtt., for instance, has been used in European floras, e.g. *Flora Europaea* vol. 1, since at least 1974, for the tall, aggressively persistent Japanese knotweed. Most North American floras including Hinds' still prefer the name *Polygonum cuspidatum* Sieb. & Zucc. for this species. *Rumex thyrsiflorus* Fingerh., a rapidly spreading European weed in eastern Canada, is morphologically a distinct species, but Hinds prefers to treat it as a subspecies of *Rumex acetosa* L. Hinds' flora is the first flora to accord due prominence to the hybrids between *Picea mariana* (Mill.) BSP. and *Picea rubens* Sarg. Trees involving some degree of hybridity between these species occur over extensive areas of New Brunswick and Nova Scotia, being in many places more abundant than either of the parent species. *Polygonum* section *Polygonum* in the flora will need revision in the light of Wolf and McNeill's study (Rhodora 88: 457-479, 1986) which greatly clarifies the taxonomy of this section and adds two species, *Polygonum franktonii* Wolf & McNeill, and *P. buxiforme* Small, to the plants of New Brunswick. The account of *Atriplex* in New Brunswick is the first accurate and up-to-date treatment of this genus to appear in any eastern North American flora.

Following a list of 25 references is an illustrated glossary with 73 line-drawings, prepared especially for the flora. The drawings are good, and they clearly depict the parts of the plant described. The index to scientific and common names, which follows, is sandwiched between the glossary and the illustrations section. This position makes the index somewhat more difficult to access than had it been placed at the end of the book.

More than 90% of the approximately 1,600 species treated are illustrated by 1,449 line-drawings, taxonomically grouped, 12 to a page, in a section following the index. The illustrations here are

reprinted from various sources, but most are reproduced in smaller size, from the 1913 edition of Britton and Brown's *An Illustrated Flora of the Northern United States and Canada.* Despite their reduction, the drawings are for the most part as clear as the originals. The only error I noticed was that the drawing labeled *Atriplex laciniata* L. depicts instead the seed and bracteoles of *Atriplex rosea* L., a central European weed unknown in New Brunswick and unable to mature seed outdoors in Maritime Canada.

The final section of the flora consists of 1,008 distribution maps, 12 to a page, based on specimens from New Brunswick, housed in several herbaria. Like the maps in many U.S. state floras, the *Flora of New Brunswick* maps show the province floating, island-like, with no relation to adjacent jurisdictions. Users of the flora, especially those from outside New Brunswick, might have found it easier to visualize species distributions had the author included at least one map showing the province in context with the rest of Maritime Canada and Northeastern Maine.

The numerous high quality illustrations and carefully constructed keys should make this flora of interest to both amateur and professional botanists, and anyone with even a casual interest in the region's higher plants. Those interested in the broader aspects of floristic botany and phytogeography will find this flora an important and useful reference.

The price, $30.00 Canadian, is very reasonable for a scientific manual of this detail and breadth. No university library or botany department should be without a copy.

PIERRE M. TASCHEREAU
SCHOOL FOR RESOURCE AND ENVIRONMENTAL STUDIES
DALHOUSIE UNIVERSITY
HALIFAX, NS, CANADA B3H 3E2

RHODORA, Vol. 90, No. 864, 1988

BOOK REVIEW

Ireland, Robert R. and Gilda Bellolio-Trucco. *Illustrated Guide to Some Hornworts, Liverworts and Mosses of Eastern Canada.* Glossary and Structure Illustrations by Linda M. Ley. Syllogeus No. 62. Botany Division, National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario, K1A 0M8. Syllogeus No. 62. 205 pp., 129 plates. No charge.

The challenge to amateur naturalists, ecologists, and teachers with an interest in hornworts, liverworts and mosses (bryology) is the quasi-microscopic character of these plants. The field of bryology needs good introductory guides to the identification of its subjects, and, wthin certain limits, this booklet goes a long way to satisfy that need. The limits, imposed by the authors, are two: firstly geographic, being all of eastern Canada from Newfoundland to southern Manitoba below 50° N latitude, and secondly, the number of species represented, 235 species out of a possible 753 reported for the area. Enough of the life cycle of mosses and general morphology of each of the major divisions is described, defined and illustrated to acquaint the reader with the structures used in identification. A section dealing with collecting techniques and preparation of a reference herbarium, critical to any satisfactory, prolonged study of these plants, is thorough. The section on identification and methods of study should be read before field work is undertaken. The booklet is spiral-bound so pages lie flat an advantage in a laboratory setting.

The keys make up the bulk of the text. They are arranged so that the three divisions, hornworts, liverworts and mosses, are distinguished first, then the genera within each division, and lastly, the species within each genus. In many cases, especially for the mosses, fruiting material is required to progress in the keys, mainly because capsules provide additional macroscopic characters by which the plants can be distinguished. The illustrations are grouped at the end of each division and the general ecology and range are given for each species. The world range of each is not indicated, but occurrences in Canadian provinces and in the United States are noted. Additional morphological description required for identification is left to the illustrations, which are restricted to macroscopic details. The illustrations, which are lavish (generally two species per full

page plate in a large 8 1/2 × 11 inch format), are a great source of descriptive information not provided by the brief text allotted to each species.

This booklet will be of greatest value to the user if it is viewed as an introduction to the identification of bryophytes, rather than as a reference manual. Less than half of the bryophyte flora of eastern Canada is treated: the user could encounter one of the 518 species not treated in this text and even (mis)identify it using the keys, as the authors readily acknowledge. Most taxa (especially mosses) require higher levels of magnification, greater morphological detail (*e.g.* sexuality) and skillful manipulation (*e.g.* cross-sectioning) to be identified with certainty, than are required in this text. The inclusion of most species in the text seems to be based on how common they are and how conspicuous the nature of their distinguishing characters.

This is an excellent first step into an area of study many people find daunting and difficult to enter, mainly because few resources exist for the beginning bryologist or interested student. Use of this text will satisfactorily familiarize the worker with these ubiquitous little plants and begin to make order out of apparent chaos. Becoming familiar with technical terms used in bryological texts, used throughout this booklet and amply treated in the extensive glossary with its full page illustrations, will also assist the user in approaching the few technical references listed by the authors which allow the identification of bryophytes with confidence.

Perhaps the most valuable contribution is the treatment of 79 species of liverworts (about half of those reported for the study area), for which there is, for the beginner, even less literature than mosses. Indeed, if the text were generated for camera-ready copy with a computer and daisy-wheel printer, as it appears to have been, we might look forward to a second edition with expanded treatments of these taxa, and more species included. Perhaps we could see the third hornwort of the three reported for the area (two are given in the text).

This booklet would also be of interest to natural history institutions who seek examples of inexpensive, high-quality publication formats of educational materials in the natural sciences as part of their educational mission to the public. The Syllogeus Series, of the number of publications issued by the National Museums of Canada, works "in the interests of making information available quickly" by

abbreviating "normal publishing procedures" without sacrificing quality of information.

This booklet will be valued by those interested in natural history, by amateur and student bryologists, and by ecologists, as well as by individuals involved in recording, protecting and understanding species diversity.

P. M. ECKEL
CLINTON HERBARIUM
BUFFALO MUSEUM OF SCIENCE
BUFFALO, NY 14214

PENN'S MORRIS ARBORETUM NAMED THE OFFICIAL ARBORETUM OF THE COMMONWEALTH OF PENNSYLVANIA

Governor Robert P. Casey has signed into law a bill designating the Morris Arboretum of the University of Pennsylvania the official arboretum of the Commonwealth of Pennsylvania.

In establishing the new designation, House Bill 1071 recognizes the Morris Arboretum "as a unique cultural resource (that)...is the oldest, most extensive curated collection of trees and shrubs cultivated for scientific and educational purposes for study and propagation in this Commonwealth."

The bill was signed on April 29—Arbor Day, a nationally recognized day for planting trees.

Dr. William M. Klein, director of the Arboretum, said the most compelling reason for naming a state arboretum was "the position of the Arboretum between the academic community and state agencies. That is, at a time when information is being gathered at a rapid rate, there is a need for specially identified institutions research centers that operate as intermediaries between state agencies in the business of resource management, and the educational institutions conducting research and teaching students."

NEBC AWARD
FOR THE SUPPORT OF BOTANICAL RESEARCH

The New England Botanical Club will again offer an award of $1000 in support of botanical research to be conducted in relation to the New England flora during 1989. This award is made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany, biosystematics, and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora*, the Club's journal, for possible publication--subject to standard review processes.

Applicants should submit a proposal of no more than three double spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1989 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138

The recipient of the award will be notified by 30 April 1989.

REVIEWERS OF MANUSCRIPTS
JULY 31, 1987 – JULY 31, 1988

The editors of RHODORA are grateful to each of the following specialists for their participation in the review process.

John H. Beaman
Ralph Brooks
Vivienne Cassie-Cooper
Paul M. Catling
Eric A. Christenson
George L. Church
David S. Conant
Wayne H. Davis
William S. Davis
William H. Drury
George S. Ellmore
W. Donald Hudson
Hugh H. Iltis
Almut G. Jones
Samuel B. Jones, Jr.
Richard LeBlond
Thomas Lee
Arthur C. Mathieson
Leslie J. Mehrhoff
Norton G. Miller
James D. Montgomery
Alexander F. Motten
Reed C. Rollins
John C. Semple
Bruce A. Sorrie
Lisa A. Standley
Fred Taylor
Edward C. Theriot
Francis R. Trainor
Sam P. VanderKloet
Gary VanWart
Edward G. Voss
Michael J. Wynne

RHODORA

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

NORTON H. NICKERSON, Editor-in-Chief
JOAN Y. NICKERSON, Managing Editor

Associate Editors

DAVID BARRINGTON
A. LINN BOGLE
DAVID E. BOUFFORD
WILLIAM D. COUNTRYMAN
GARRETT E. CROW
RICHARD A. FRALICK
GERALD J. GASTONY
C. BARRE HELLQUIST
MICHAEL W. LEFOR
ROBERT T. WILCE

VOLUME 90

1988

The New England Botanical Club, Inc.

Harvard University Herbaria, 22 Divinity Ave., Cambridge, Mass. 02138

INDEX TO VOLUME 90

New scientific names are in **bold face**.

Acer (Maple) species, sections Acer and Goniocarpa. New chromosome counts in, 127–131
Adicea (Urticaceae). Typification of J. Lunell's names in, 123 125
ANNOUNCEMENTS:
Jesse M. Greenman Award 103
NEBC: Award 352; Notice for 1989 476
Herbarium Acquisition Policy 105 109
Symposium 104
Penn's Morris Arboretum named official arboretum of the Commonwealth of Pennsylvania. 475
Antennaria (Asteraceae: Inuleae) in western North America. The genus, II. Additional chromosome counts. 133–137
Argentina and Bolivia and the status of C. phalaroides var. parvula in southern South America. A first report for Carex hypsipedos (Cyperaceae) in, 149 155
Arnica (Asteraceae) subgenus Arctica. Taxonomy of, 245–275
Aster nemoralis is extant in Vermont. 339 340

Bain, John F. Taxonomy of Senecio streptanthifolius Greene. 277 312
Ball, Peter W. *see* Ford, Bruce A.
Benthic marine algae of southwestern New Brunswick, Canada. A survey of the, 419 451
Betula nigra at Mendum's Pond, Barrington, NH and Pawtuckaway Lake, Nottingham, NH. 345
Blondeau, Marcel *see* Cody, William J.
Bogle, A. Linn *see* Philbrick, C. Thomas
Bolivia and the status of C. phalaroides var. parvula in southern South America. A first report for Carex hypsipedos (Cyperaceae) in Argentina and, 149–155
BOOK REVIEWS:
Aquatic and Wetland Plants of Kentucky 351
Flora of New Brunswick 467 469
Flora of the Vascular Plants of Cattaraugus County, New York. A, 465 466
Illustrated Guide to Some Hornworts, Liverworts and Mosses of Eastern Canada. 471–473
Orchids of Ontario 347 349
Orchids of the Western Great Lakes Region 209–210
Seaside Plants of the Gulf and Atlantic Coasts 213
Boufford, David E. Typification of J. Lunnel's names in Adicea (Urticaceae). 123 125
Brassica in the northeastern United States. Evidence of pre-Columbian, 355 362
Buffalo clovers in Kentucky (Trifolium stoloniferum and T. reflexum): historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number. 399 418
Burk, C. John and Nancy D. McMaster. The spread of Catalpa ovata G. Don in western Massachusetts and its biogeographic implications. 461 464
Burk, C. John and Vikram Prabhu. Growth and extension of a naturalized western Massachusetts stand of Catalpa speciosa Warder. 457 459

Calopogon tuberosus var. latifolius (St John) Boivin (Orchidaceae) new to the Unted States. 101
Campbell, Julian J. N., Marc Evans, Max E. Medley and Norman L. Taylor. Buffalo clovers in Kentucky (Trifolium stoloniferum and T. reflexum): historical records, presettlement environment, rediscovery,

endangered status, cultivation and chromosome number. 399 418
Canada. A survey of the benthic marine algae of southwestern New Brunswick, 419 451
Carex hypsipedos (Cyperaceae) in Argentina and Bolivia and the status of C. phalaroides var. parvula in southern South America. A first report for, 149 155
Carex phalaroides var. parvula in southern South America. A first report for Carex hypsipedos (Cyperaceae) in Argentina and Bolivia and the status of, 149 155
Catalpa ovata G. Don in western Massachusetts and its biogeographic implications. The spread of, 461-464
Catalpa speciosa Warder. Growth and extension of a naturalized western Massachusetts stand of, 457 459
Catling, Paul M. and Vivian R. Catling. Spiranthes nebulorum (Orchidaceae), a new species from southern Mexico and Guatemala. 139 147
Catling, Vivian R. *see* Catling, Paul M.
Cayouette, Jacques *see* Cody, William J.
Chmielewski, J. G. and C. C. Chinnappa. The genus Antennaria (Asteraceae: Inuleae) in western North America. II. Additional chromosome counts. 133-137
Chimaphila. Reproductive biology of two sympatric species of, 233-244
Chinnappa, C. C. *see* Chmielewski, J. G.
Chromosome counts in Acer (Maple) species, sections Acer and Goniocarpa. New, 127 131
Cody, William J., Marcel Blondeau and Jacques Cayouette. Ranunculus Xspitzbergensis (Nath.) Hadač, an addition to the flora of North America. 27 36
Cormier, Charles R. Betula nigra at Mendum's Pond, Barrington, NH and Pawtuckaway Lake, Nottingham, NH. 345
Correct name for Elliott's Goldenrod. The, 157-168
Davenport, L. J. A monograph of Hydrolea (Hydrophyllaceae). 169 208
Denford, Keith E. *see* Downie, Stephen R.
Description and distribution of Euphrasia stricta in North America. 223 231
Diatoms, freshwater, (Bacillariophyceae) from the northeastern Glacial Lake District of Wisconsin. II. Cymbellonitzschia, Hantzschia, and Nitzschia (Order Pennales, Family Nitzschiaceae). 379 397
Distribution of Euphrasia stricta in North America. Description and, 223 231
Downie, Stephen R. and Keith E. Denford. Taxonomy of Arnica (Asteraceae) subgenus Arctica. 245-275
Downie, Stephen R. and John McNeill. Description and distribution of Euphrasia stricta in North America. 223 231
Dryopteris fragrans in Vermont. Two new stations for, 455 456

Eastman, Leslie. Calopogon tuberosus var. latifolius (St. John) Boivin (Orchidaceae) new to the United States. 101
Elliott's Goldenrod. The correct name for, 157 168
Euphrasia stricta in North America. Description and distribution of, 223 231
Europe. A reevaluation of the Triglochin maritimum complex (Juncaginaceae) in eastern and central North America and, 313 337
Evans, Marc *see* Campbell, Julian J. N.
Evidence of pre-Columbian Brassica in the northeastern United States. 355 362

Farnham, W. F. *see* South, G. Robin
Fenwick, Mason G. Morphological variability of a Scenedesmus denticulatus Lagerh. isolate in culture and some taxonomic revisions. 363 368
First report for Carex hypsipedos (Cy-

peraceae) in Argentina and Bolivia and the status of C. phalaroides var. parvula in South America. A, 149–155
Floral variation in five populations of Podostemum ceratophyllum Michx. (Podostemaceae). A survey of, 113–121
Floristic inventory of the Gateway National Recreation Area, New York — New Jersey. A, 21–26
Ford, Bruce A. and Peter W. Ball. A reevaluation of the Triglochin maritimum complex (Juncaginaceae) in eastern and central North America and Europe. 313–337
Freshwater diatoms (Bacillariophyceae) from the northeastern glacial lake district of Wisconsin. II. Cymbellonitzschia, Hantzschia, and Nitzschia (Order Pennales, Family Nitzschiaceae). 379–397

Gateway National Recreation Area, New York — New Jersey. Floristic inventory of the, 21–26
Genus Antennaria (Asteraceae: Inuleae) in western North America, The, II. Additional chromosome counts. 133–137
Gilman, Arthur V. Two new stations for Dryopteris fragrans in Vermont. 455–456
Goniocarpa. New chromosome counts in Acer (Maple) species, sections Acer and, 127–131
Greller, Andrew *see* Stalter, Richard
Growth and extension of a naturalized western Massachusetts stand of Catalpa speciosa Warder. 457–459
Guatemala. Spiranthes nebulorum (Orchidaceae), a new species from southern Mexico and, 139–147

Hellquist, C. Barre, C. Thomas Philbrick and Robert L. Hilton. The taxonomic status of Potamogeton lateralis Morong (Potamogetonaceae). 15–20
Herbarium acquisition policy, NEBC 105–109
Hilton, Robert L. *see* Hellquist, C. Barre
Hispaniola. A new Pilea (Urticaceae) from, 215–222
Hjersted, Ingrid M. *see* Standley, Lisa A.
Hydrolea (Hydrophyllaceae). A monograph of, 169–208
Hydrolea spinosa var. **maior** (Brand) Davenport *comb. nov.* 187

Jacobson, Heather A., James B. Petersen and David E. Putnam. Evidence of pre-Columbian Brassica in the northeastern United States. 355–362
Johnson, David M. and Nancy A. Murray. Polemonium vanbruntiae (Polemoniaceae) in Maine. 453–455
Judd, Walter S. *see* Skean, James D.

Kadereit, Joachim W. Papaver L. sect. Californicum Kadereit, a new section of the genus. 7–13
Keats, D. W. *see* South, G. Robin
Kentucky, buffalo clovers in, (Trifolium stoloniferum and T. reflexum): historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number. 399–418
Kim, Sarah S.-H. *see* Standley, Lisa A.
Kudzu (Pueraria lobata) in New England. 341–343

Lewis, Walter H. Regrowth of a decimated population of Panax quinquefolium in a Missouri climax forest. 1–5
Lipsey, Louis L., Jr. Freshwater diatoms (Bacillariophyceae) from the northeastern glacial lake district of Wisconsin. II. Cymbellonitzschia, Hantzschia, and Nitzschia (Order Pennales, Family Nitzschiaceae). 379–397

Maine. Polemonium vanbruntiae (Polemoniaceae) in, 453–454
Massachusetts stand of Catalpa speciosa Warder. Growth and extension of a

naturalized western, 457 459
Massachusetts. The spread of Catalpa ovata G. Don in western, and its biogeographic implications. 461–464
McMaster, Nancy D. *see* Burk, C. John
McNeill, John *see* Downie, Stephen R.
Medley, Max E. *see* Campbell, Julian J. N.
Mexico, southern, and Guatemala. Spiranthes nebulorum (Orchidaceae), a new species from, 139 147
Minnesota. New and noteworthy plant records for, 369–377
Missouri climax forest. Regrowth of a decimated population of Panax quinquefolium in a, 1 5
Monograph of Hydrolea (Hydrophyllaceae). A, 169 208
Morphological variability of a Scenedesmus denticulatus Lagerh. isolate in culture and some taxonomic revisions. 363 368
Murray, Nancy A. *see* Johnson, David M.

NEBC Herbarium acquisition policy 105 109
New and noteworthy plant records for Minnesota. 369 377
New Brunswick, Canada. A survey of the benthic marine algae of southwestern, 419 451
New chromosome counts in Acer (Maple) species, sections Acer and Goniocarpa. 127 131
NEW ENGLAND NOTES:
Aster nemoralis is extant in Vermont. 339 340
Betula nigra at Mendum's Pond, Barrington, NH and Pawtuckaway Lake, Nottingham, NH. 345
Calopogon tuberosus var. latifolius (St. John) Boivin Orchidaceae new to the United States. 101
Growth and extension of a naturalized western Massachusetts stand of Catalpa speciosa Warder. 457–459
Kudzu (Pueraria lobata) in New England. 341 343
Polemonium vanbruntiae (Polemoniaceae) in Maine. 453 454
Spread of Catalpa ovata G. Don in western Massachusetts and its biogeographic implications. The, 461 464
Two new stations for Dryopteris fragrans in Vermont. 455 456

New Hampshire. Betula nigra at Mendum's Pond, Barrington, NH and Pawtuckaway Lake, Nottingham, NH. 345
New York – New Jersey. Floristic inventory of the Gateway National Recreation Area, 21 26
North America. Description and distribution of Euphrasia stricta in, 223 231
North America. Ranunculus Xspitzbergensis (Nath.) Hadač, an addition to the flora of, 27 36
North America and Europe. A reevaluation of the Triglochin maritimum complex (Juncaginaceae) in eastern and central, 313–337
North America, western. The genus Antennaria (Asteraceae:Inuleae) in, II. Additional chromosome counts. 133–137

Ownbey, Gerald B. and Welby R. Smith. New and noteworthy plant records for Minnesota. 369 377

Panax quinquefolium in a Missouri climax forest. Regrowth of a decimated population of, 1–5
Papaver L. sect. Californicum Kadereit, a new section of the genus. 7 13
Papaver sect. **Californicum** Kadereit, *sect. nov.* 11, fig. 9
Perkins, William D. *see* Sorrie, Bruce A.
Petersen, James B. *see* Jacobson, Heather A.
Philbrick, C. Thomas. *see* Hellquist, C. Barre
Philbrick, C. Thomas and A. Linn Bogle. A survey of floral variation in five populations of Podostemum cer-

atophyllum Michx. (Podostemaceae). 113–121
Pilea (Urticaceae) from Hispaniola. A new, 215 222
Pilea howardiana Skean & Judd, *sp. nov.* 216, fig. 219.
Plant records for Minnesota. New and noteworthy, 369 377
Podostemum ceratophyllum Michx. (Podostemaceae). A survey of floral variation in five populations of, 113–121
Polemonium vanbruntiae (Polemoniaceae) in Maine. 453–454
Porter, Duncan M. *see* Uttal, Leonard J.
Potamogeton lateralis Morong (Potamogetonaceae). The taxonomic status of, 15–20
Prabhu, Vikram *see* Burk, C. John
(Pueraria lobata) in New England. Kudzu, 341 343
Putnam, David E. *see* Jacobson, Heather A.

Ranunculus Xspitzbergensis (Nath.) Hadač, an addition to the flora of North America. 27 36
Reevaluation of the Triglochin maritimum complex (Juncaginaceae) in eastern and central North America and Europe. A, 313–337
Regrowth of a decimated population of Panax quinquefolium in a Missouri climax forest. 1 5
Reproductive biology of two sympatric species of Chimaphila. 233–244
Reviewers, List of 476

Santamour, Jr. Frank S.
Scenedesmus denticulatus Lagerh. isolate in culture and some taxonomic revisions. Morphological variability of a, 363 368
Senecio streptanthifolius Greene. Taxonomy of, 277–312
Skean, James D. and Walter S. Judd. A new Pilea (Urticaceae) from Hispaniola. 215–222
Smith, Welby R. *see* Ownbey, Gerald B.
Sorrie, Bruce A. and William D. Perkins. Kudzu (Pueraria lobata) in New England. 341 343
South America, southern, A first report for Carex hypsipedos (Cyperaceae) in Argentina and Bolivia and the status of C. phalaroides var. parvula in, 149 155
South, G. Robin, I. Tittley, W. F. Farnham and D. W. Keats. A survey of the benthic marine algae of southwestern New Brunswick, Canada. 419 451
Spiranthes nebulorum (Orchidaceae), a new species from southern Mexico and Guatemala. 139 147
Spread of Catalpa ovata G. Don in western Massachusetts and its biogeographic implications. 461 464
Spiranthes nebulorum Catling & Catling *sp. nov.* 139, fig. 141
Stalter, Richard and Andrew Greller. Floristic inventory of the Gateway National Recreation Area, New York New Jersey.
Standley, Lisa A., Sarah S. -H. Kim and Ingrid M. Hjersted. Reproductive biology of two sympatric species of Chimaphila. 233 244
Stutts, John G. Taxonomic revision of Vernonia subsect. Chamaedrys (Compositae: Vernonieae). 37–99
Survey of floral variation in five populations of Podostemum ceratophyllum Michx. (Podostemaceae). A, 113 121
Survey of the benthic marine algae of southwestern New Brunswick, Canada. A, 419–451. Chlorophyceae 421; Cyanophyceae 440; Phaeophyceae 429; Rhodophyceae 434; Xanthophyceae 441
Sympatric species of Chimaphila. Reproductive biology of two, 233 244

Taxonomic revision of Vernonia subsect. Chamaedrys (Compositae: Vernonieae). 37 99.
Part I: Exclusions and new infrageneric taxa 40;
series **Brasilianae** Stutts, *ser. nov.* 41

subseries **Chaquenses** Stutts, *subser. nov.* 44
subseries **Laxae** Stutts, *subser. nov.* 43
series **Nitidulae** (Cabrera) Stutts, *stat. nov.* 42
series **Puberulae** Stutts, *ser. nov.* 45
series **Tomentellae** Stutts, *ser. nov.* 41
Part II: Chemosystematics, palynology, cytology, and hybridization 45;
Part III: Taxonomic treatment 65.

Taxonomic status of Potamogeton lateralis Morong (Potamogetonaceae). The, 15 20
Taxonomy of Arnica (Asteraceae) subgenus Arctica. 245 275
Taxonomy of Senecio streptanthifolius Greene. 277 312
Key to the varieties of Senecio streptanthifolius 286
var. **borealis** (T. & G.) J. F. Bain *comb. nov.* 293
var. **kluanei** J. F. Bain *var. nov.* 297
var. **laetiflorus** (Greene) J. F. Bain *comb. nov.* 302
var. **oodes** (Rydberg) J. F. Bain *comb. nov.* 308
var. **rubricaulis** (Greene) J. F. Bain *comb. nov.* 299
var. **wallowensis** J. F. Bain *var. nov.* 306
Taylor, Norman L. *see* Campbell, Julian J. N.
Tittley, I. *see* South, G. Robin
Triglochin maritimum complex (Juncaginaceae) in eastern and central North America and Europe. A reevaluation of the, 313 337
(Trifolium stoloniferum and T. reflexum), Buffalo clovers in Kentucky: historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome numbers. 399 418
Two new stations for Dryopteris fragrans in Vermont. 455 456
Typification of J. Lunell's names in Adicea (Urticaceae). 123 25

United States. Calopogon tuberosus var. latifolius (St. John) Boivin (Orchidaceae) new to the, 101
United States. Evidence of pre-Columbian Brassica in the northeastern, 355 362
Uttal, Leonard J. and Duncan M. Porter. The corect name for Elliott's Goldenrod. 157 168

Vermont. Aster nemoralis is extant in, 339 340
Vermont. Two new stations for Dryopteris fragrans in, 455 456
Vernonia subsect. Chamaedrys (Compositae: Vernonieae). Taxonomic revision of, 37 99

Wheeler, Gerald A. A first report for Carex hypsipedos (Cyperaceae) in Argentina and Bolivia and the status of C. phalaroides var. parvula in southern South America. 149 155
Wisconsin. Freshwater diatoms (Bacillariophyceae) from the northeastern glacial lake district of, II. Cymbellonitzschia, Hantzschia, and Nitzschia (Order Pennales, Family Nitzschiaceae). 379 397

Zika, Peter F. Aster nemoralis is extant in Vermont. 339 340

Vol 90, No. 863, including pages 215–353, was issued August 26, 1988

The New England Botanical Club
22 Divinity Avenue
Cambridge, Mass. 02138

The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 90th year and contains about 500 pages a volume.

Membership is open to all persons interested in systematics and field botany. Annual dues are $25.00, including a subscription to RHODORA. Students may apply for a Student Membership at $10.00 a year, which does not include a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

Regular Member	$25.00
Family Membership	$35.00
Student Member	$10.00
For this calendar year	_____
For the next calendar year	_____

Name _____

Address _____

City & State _____ Zip _____

Special interests (optional):

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8″) **throughout** including tables, figure legends, and literature citations. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

U.S. Postal Service

STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

Required by 39 U.S.C. 3685)

1A. TITLE OF PUBLICATION	1B. PUBLICATION NO.	2. DATE OF FILING
RHODORA	0 0 3 5 4 9 0 2	Sept. 26, 1988
3. FREQUENCY OF ISSUE	3A. NO. OF ISSUES PUBLISHED ANNUALLY	3B. ANNUAL SUBSCRIPTION PRICE
Quarterly	4	$30.00

4. COMPLETE MAILING ADDRESS OF KNOWN OFFICE OF PUBLICATION *(Street, City, County, State and ZIP+4 Code) (Not printers)*
New England Botanical Club,Inc.,c/o Harvard University Herbarium,22 Divinity Ave, Cambridge,MA 02138

5. COMPLETE MAILING ADDRESS OF THE HEADQUARTERS OF GENERAL BUSINESS OFFICES OF THE PUBLISHER *(Not printer)*
New England Botanical Club,Inc.,c/o Harvard University Herbarium, 22 Divinity Ave, Cambridge,MA 02138

6. FULL NAMES AND COMPLETE MAILING ADDRESS OF PUBLISHER, EDITOR, AND MANAGING EDITOR *(This item MUST NOT be blank)*

PUBLISHER *(Name and Complete Mailing Address)*
New England Botanical Club,Inc.,c/o Harvard University Herbarium,22 Divinity Ave, Cambridge,MA 02138

EDITOR *(Name and Complete Mailing Address)*
Prof. Norton H. Nickerson, Tufts University-Biology, Medford,MA 02155

MANAGING EDITOR *(Name and Complete Mailing Address)*
Joan Y. Nickerson,Tufts University-Biology, Medford,MA 02155

7. OWNER *(If owned by a corporation, its name and address must be stated and also immediately thereunder the names and addresses of stockholders owning or holding 1 percent or more of total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address, as well as that of each individual must be given. If the publication is published by a nonprofit organization, its name and address must be stated.) (Item must be completed.)*

FULL NAME	COMPLETE MAILING ADDRESS
New England Botanical Club, Inc.	c/o Harvard University Herbarium, 22 Divinity Ave., Cambridge, MA 02138

8. KNOWN BONDHOLDERS, MORTGAGEES, AND OTHER SECURITY HOLDERS OWNING OR HOLDING 1 PERCENT OR MORE OF TOTAL AMOUNT OF BONDS, MORTGAGES OR OTHER SECURITIES *(If there are none, so state)*

FULL NAME	COMPLETE MAILING ADDRESS
NONE	

9. FOR COMPLETION BY NONPROFIT ORGANIZATIONS AUTHORIZED TO MAIL AT SPECIAL RATES *(Section 423.12 DMM only)*
The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes *(Check one)*

☒ (1) HAS NOT CHANGED DURING PRECEDING 12 MONTHS

☐ (2) HAS CHANGED DURING PRECEDING 12 MONTHS *(If changed, publisher must submit explanation of change with this statement.)*

10. EXTENT AND NATURE OF CIRCULATION *(See instructions on reverse side)*	AVERAGE NO. COPIES EACH ISSUE DURING PRECEDING 12 MONTHS	ACTUAL NO. COPIES OF SINGLE ISSUE PUBLISHED NEAREST TO FILING DATE
A. TOTAL NO. COPIES *(Net Press Run)*	1000	1000
B. PAID AND/OR REQUESTED CIRCULATION 1. Sales through dealers and carriers, street vendors and counter sales	575	575
2. Mail Subscription *(Paid and/or requested)*	300	300
C. TOTAL PAID AND/OR REQUESTED CIRCULATION *(Sum of 10B1 and 10B2)*	875	875
D. FREE DISTRIBUTION BY MAIL, CARRIER OR OTHER MEANS SAMPLES, COMPLIMENTARY, AND OTHER FREE COPIES	20	20
E. TOTAL DISTRIBUTION *(Sum of C and D)*	895	895
F. COPIES NOT DISTRIBUTED 1. Office use, left over, unaccounted, spoiled after printing	105	105
2. Return from News Agents	0	0
G. TOTAL *(Sum of E, F1 and 2—should equal net press run shown in A)*	1000	1000

11. I certify that the statements made by me above are correct and complete	SIGNATURE AND TITLE OF EDITOR, PUBLISHER, BUSINESS MANAGER, OR OWNER
	Herman F. Forest Bus. manager

PS Form 3526, Dec 1986 *(See instructions on reverse)*

RHODORA October 1988 Vol. 90, No. 864

CONTENTS

Evidence of pre-Columbian Brassica in the northeastern United States
Heather A. Jacobson, James B. Petersen and *David E. Putnam* . . . 355
Morphological variability of a Scenedesmus denticulatus Lagerh. isolate in culture and some taxonomic revisions
Mason G. Fenwick 363
New and noteworthy plant records for Minnesota
Gerald B. Ownbey and *Welby R. Smith* 369
Freshwater diatoms (Bacillariophyceae) from the northeastern Glacial Lake District of Wisconsin. II. Cymbellonitzschia, Hantzschia, and Nitzschia (Order Pennales, Family Nitzschiaceae)
Louis L. Lipsey, Jr. 379
Buffalo clovers in Kentucky (Trifolium stoloniferum and T. reflexum): historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number
Julian J. N. Campbell, Marc Evans, Max E. Medley and *Norman L. Taylor* 399
A survey of the benthic marine algae of southwestern New Brunswick, Canada
G. R. South, I. Tittley, W. F. Farnham and *D. W. Keats* . . . 419

NEW ENGLAND NOTES

Polemonium vanbruntiae (Polemoniaceae) in Maine
David M. Johnson and *Nancy A. Murray* 453
Two new stations for Dryopteris fragrans in Vermont
Arthur V. Gilman 455
Growth and extension of a naturalized western Massachusetts stand of Catalpa speciosa Warder
C. John Burk and *Vikram Prabhu* 457
The spread of Catalpa ovata G. Don in western Massachusetts and its biogeographic implications
C. John Burk and *Nancy D. McMaster* 461

BOOK REVIEWS

A Flora of the Vascular Plants of Cattaraugus County, New York
Norton G. Miller 465
Flora of New Brunswick
Pierre M. Taschereau 467
Illustarted Guide to Some Hornworts, Liverworts and Mosses of Eastern Canada
P. M. Eckel 471

ANNOUNCEMENTS

U Penn.'s Morris Arboretum 474
NEBC 1989 Award Notice 475
List of Reviewers 476
Index to Volume 90 477
NEBC Membership Form 485
Instructions to Contributors 486
Statement of Ownership . . . . . inside back cover